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NATURAL VARIATION IN ABUNDANCE OF SALMONID POPULATIONS IN STREAMS

A Review

by

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Literature on stock size and production of salmonid populations in streams has been reviewed. The objective is to bring together data on the magnitude of natural variation in population size and to relate this variability to environmental conditions where possible. Recommendations are presented for the use of this information in designing studies to estimate the impact of nonpoint source pollution. A number of long term studies, some up to 15-20 years, have provided useful data on temporal variation in population abundance. Other studies have examined spatial variation. Data from the best examples of both kinds of variation are presented in Appendix Tables. Temporal and spatial variation may be as high as several orders of magnitude in the extreme, and at least are sufficient to mask very significant perturbations caused by nonpoint source pollutants. Environmental variables most closely associated with spatial variation are those relating to the quality of salmonid habitat, particularly physical characteristics such as cover in its many forms. Streamflow and food abundance have been associated with both temporal and spatial variation. In general, physical characteristics of habitat seem most promising as descriptors of variability. More emphasis on study of basic processes in stream ecosystems and more extensive use of paired comparisons in design of impact studies are also suggested as a means of more clearly separating natural variation from damage caused by nonpoint source pollutants.

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ABSTRACT

Literature on stock size and production of salmonid populations in streams has been reviewed. The objective is to bring together data on the magnitude of natural variation in population size and to relate this variability to environmental conditions where possible. Recommendations are presented for the use of this information in designing studies to estimate the impact of non-point source pollution.

A number of long-term studies, some up to 15-20 years, have provided useful data on temporal variation in population abundance. Other studies have examined spatial variation. Data from the best examples of both kinds of variation are presented in Appendix Tables. Temporal and spatial variation may be as high as several orders of magnitude in the extreme, and even at the least are sufficient to mask very significant perturbations caused by non-point source pollutants. Environmental variables most closely associated with spatial variation are those relating to the quality of salmonid habitat, particularly physical characteristics such as cover in its many forms. Streamflow and food abundance have been associated with both temporal and spatial variation. In general, physical characteristics of habitat seem most promising as descriptors of variability.

Systems of rating habitat quality should receive considerable emphasis in attempts to minimize the effects of natural variation in the evaluation of impacts of non-point source pollutants. First priority should be placed on assessment of physical features. This approach has been used so far mainly to explain spatial variation, but has promise of explaining temporal variation as well, particularly in reference to fluctuation in streamflow. The other major emphasis should be in further development of systems of stream and watershed classification. The most useful of these devised to date take a perspective from geomorphology and focus on the potential of a stream system for biological production. More emphasis on study of basic processes in stream ecosystems and more extensive use of paired comparisons in design of impact studies are also suggested as means of more clearly separating natural variation from damage caused by non-point source pollutants.

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SECTION 1

INTRODUCTION

Assessment of impacts on streams caused by non-point source pollutants is now receiving increasing attention. Salmonids are the principal fish species of economic importance affected in the western United States. Assessment of damage to these populations cannot be undertaken without some understanding of natural variation in abundance within and between populations. Strategies of analysis must be devised that will separate natural variation from effects due to disturbance. It is the purpose of this review to bring together literature and unpublished data on the natural variation in abundance of salmonid populations in streams and to attempt to relate this variation to environmental variables--physical, chemical, and biological.

There are two kinds of variability to be considered, spatial and temporal. Spatial variability can be studied at several levels of resolution, ranging from microhabitat preferences to variability within and between streams. Temporal fluctuations in abundance can occur on a diel, seasonal, or annual scale.

This paper will concentrate on studies of salmonid species during that part of their lives spent in the stream environment. The species include the coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), brown trout (*Salmo trutta*), rainbow trout (*S. gairdneri*), steelhead trout (*S. gairdneri gairdneri*), cutthroat trout (*S. clarki*), Atlantic salmon (*S. salar*), brook trout (*Salvelinus fontinalis*), and Dolly Varden (*S. malma*). We began this review with the intention of emphasizing studies on the west coast of North America. However, we found that most of the quantitative data on variability in resident salmonid populations came from other areas, and much of that information has been included.

Much less information is available on population levels of the fish species associated with salmonids. Though not included here, the importance of this element of the aquatic system should be emphasized and steps taken to fill this gap in our knowledge of stream fish communities.

SECTION 2

CONCLUSIONS AND RECOMMENDATIONS

The standing stock biomass of salmonid fishes in streams shows great natural variation, both in time and space. Reported levels of biomass vary from zero or just above to just over $60\ g/m^2$. This variation is sufficient to mask large-scale perturbations caused by non-point source pollutants, such as result from logging and agricultural practices. Among the most important causes of variation are differences in physical characteristics of streams, including streamflow and habitat quality, particularly cover. Biological factors, such as food abundance and predation, may sometimes influence abundance, but their mode of action is less clear and the case for their involvement more equivocal than that of the physical elements of the habitat.

We recommend several courses of action that will help to minimize the effects of this natural variation when attempts are made to evaluate impacts of a particular non-point source pollutant. Habitat quality rating systems are being developed that show promise of explaining much of the spatial variation in salmonid populations in streams. These rating systems are based primarily on assessment of physical features. They may also help to explain temporal variation caused by changes in streamflow, but other influences on temporal variation need further study. The other major approach that may aid impact assessment is development of schemes of stream and watershed classification, such as those of Platts (1974) and Warren (1979). The latter is particularly promising in that it focuses on the potential of a system for biological production, rather than a particular value of the moment, and takes a biogeoclimatic perspective. Continuing emphasis on study of the basic physical and biological processes that lead to growth, mortality, and production of stream salmonids is another promising approach to understanding natural variation in abundance. Finally, new approaches to the design of impact studies are suggestd that may aid in more clearly separating natural variation from that caused by non-point source pollutants and in monitoring the time required for biological systems to recover from perturbation.

SECTION 3

STUDIES OF VARIABILITY

Natural variability of salmonid populations in streams has been measured by two principal methods. In some streams, weirs or traps have been constructed to get reliable counts of migrating fish. Other studies have examined standing crops in the stream by electroshocking, netting, or angling.

There have been a number of important long-term studies on natural variation in abundance of anadromous and resident species, which are briefly described in Table 1. As an aid to further analysis, data from these studies and others of shorter duration that deal with spatial variation have been compiled from original sources and are included in tables in the Appendix. Further description of many studies is included in the annotated bibliography.

We performed some preliminary analyses on the data in the Appendix Tables and in other publications, in search of general patterns in variation over the species and geographical areas included. We used the range in abundance as a fraction of mean abundance for a measure of relative variability, rather than the coefficient of variation, owing to small sample sizes. Not surprisingly, the extremes of temporal variation occur in pink and chum salmon fry; their numbers may vary over several orders of magnitude. The most stable populations are those of brook trout in Wisconsin and Michigan, where the range is in the order of only one-half the mean abundance. Notably, two of the most useful analyses of variation and its causes were from these two populations (McFadden et al. 1967; Hunt 1974). Where good comparisons of both temporal and spatial variation could be made in the same stream system (Sagehen Creek, California and Lawrence Creek, Wisconsin), spatial variation was the greater, by a significant margin. This, again, may not be a surprising result, but is one with important implications for impact studies.

It appears that inferences about natural fluctuation in abundance and its causes may best be found in detailed analyses of individual research studies, including information on as many relevant environmental variables as possible. Thus the bulk of this review is concerned with attempts to relate variation in abundance to the environmental factors with which it may be associated.

TABLE 1. LONG-TERM STUDIES OF STREAM SALMONID POPULATIONS.

Location	Species	Inclusive Dates for Data Presented	Principal Reference
Sashin Creek, Alaska	pink salmon coho salmon	1940-1959 1956-1968	Merrell (1962) Crone and Bond (1976)
Hooknose Creek, British Columbia	pink salmon chum salmon	1947-1956	Hunter (1959)
Carnation Creek, British Columbia	coho salmon cutthroat trout steelhead trout	1970-1977 (continuing)	Nawer and Andersen (1974)
Minter Creek, Washington	coho salmon	1938-1953	Salo and Bayliff (1958)
Alsea River, Oregon	coho salmon cutthroat trout	1959-1973	Moring and Lantz (1975) Knight (1980)
Waddell Creek, California	coho salmon steelhead trout	1933-1944	Shapovalov and Taft (1954)
Sagehen Creek, California	rainbow trout brown trout brook trout	1952-1961	Gard and Flittner (1974)
Lawrence Creek, Wisconsin	brook trout	1953-1970	Hunt (1974)
Hunt Creek, Michigan	brook trout	1949-1962	McFadden et al. (1967)
Au Sable River, Michigan	brook trout brown trout	1957-1967	Alexander (1979)
Hayes Brook, Prince Edward Island	brook trout	1947-1960	Saunders and Smith (1962)
Little Codroy River, Newfoundland	Atlantic salmon brook trout	1954-1963	Murray (1968)
Shelligan Burn, Scotland	Atlantic salmon brown trout	1966-1975	Egglishaw and Shackley (1977)

SECTION 4

FACTORS AFFECTING NATURAL VARIABILITY

One approach to listing the important factors or variables in the stream environment that can affect abundance of salmonid populations is the following:

A. Physical factors

   1. Streamflow
   2. Habitat quality

B. Biological factors

   1. Food abundance
   2. Predation
   3. Movement and migration

In most instances these variables may interact to influence a population, and the classification is inevitably artificial. For example, habitat preferences are often related to food availability. Under natural conditions, it is often difficult to measure the effect of one factor independently. However, the variables will be considered separately in this discussion, with an attempt to show how interactions may be involved.

PHYSICAL FACTORS

Streamflow

One of the earliest studies that attempted to relate streamflow to salmonid abundance was conducted by McKernan et al. (1950). They found that low summer flows correlated with subsequent low returns of adult coho salmon in the Siletz River, Oregon from 1924 to 1945. No relation was apparent in the Coquille River from 1923 to 1948. Scarnecchia (1978) found a significant correlation ($r = 0.68$) between total streamflow in the 17-month period of stream residence of juvenile coho and the commercial troll catch of adult salmon 2 years later. These data came from five Oregon rivers from 1942 to 1962. In addition, there was a significant correlation ($r = 0.56$) between total annual flow and catch 2 years later. Smoker (1955) obtained an even higher correlation ($r = 0.91$) in the same analysis (total annual flow vs. catch of adult coho 2 years later) for Puget Sound streams from 1935 to 1954. In Cowichan Bay, B. C., a lower availability of coho to the sport fishery was noted for year classes that experienced low summer streamflows in their juvenile stages (Neave 1949). In Nile Creek, B. C., from 1946 through 1949 the output of coho smolts varied directly with the minimum monthly rainfall during the previous summer (Wickett 1951). These studies show that streamflow during some part of the freshwater phase of coho life history can influence its level of abundance of the pop in the catch.

We carried out a similar analysis for juvenile coho salmon in two of the streams that were part of the Alsea Watershed Study in Oregon. Mean monthly and seasonal discharge were correlated with mean June-April biomass and also with the smolt count in the same period, from June 1960 through May 1968. In both streams the few significant correlations were mostly in the spring (Table 2).

TABLE 2. CORRELATIONS BETWEEN MEAN MONTHLY DISCHARGE AND ANNUAL SMOLT COUNT AND MEAN JUNE-APRIL BIOMASS FOR COHO SALMON, ALSEA WATERSHED STUDY, JUNE 1960-MAY 1969.

	Deer Cr.		Flynn Cr.	
Period	Smolt	Biomass	Smolt	Biomass
June	-0.080	-0.080	-0.307	-0.321
July	0.095	-0.442	-0.004	-0.126
August	0.050	-0.199	-0.155	-0.267
September	0.098	-0.045	-0.206	-0.221
October	0.431	0.661	-0.122	0.145
November	-0.076	-0.461	0.132	0.032
December	0.153	0.003	0.291	-0.373
January	-0.398	-0.218	0.531	-0.654
February	-0.099	-0.006	0.042	0.088
March	-0.687*	-0.426	0.099	-0.055
April	0.630	0.076	0.931**	0.936**
May	0.569	-0.162	0.714*	0.694*
June-May	-0.350	-0.507	0.150	-0.364
Nov-Apr	-0.482	-0.544	-0.209	-0.446
Jan-Apr	-0.691*	-0.448	-0.097	-0.279
Mar-Apr	-0.344	-0.352	0.518	0.385
June-Sept	-0.021	-0.125	-0.262	-0.230

* $P < 0.05$

** $P < 0.01$

Knight (1980) used a longer series of data on smolt abundance alone and found significant negative correlations between mean January discharge and total November-May smolt count for Deer Creek and Flynn Creek (r = -0.64 and -0.65 respectively) for the 1959-1960 through 1972-1973 seasons. We performed a similar analysis for cutthroat trout from September biomass data and mean monthly discharge data (October 1961-September 1972) for all three streams in the Alsea Watershed Study. Generally, correlations were negative, but nonsignificant, in the winter months in all three streams (Table 3).

TABLE 3. CORRELATIONS BETWEEN MEAN MONTHLY DISCHARGE AND MEAN SEPTEMBER BIOMASS IN G/M^2 FOR CUTTHROAT TROUT, ALSEA WATERSHED STUDY, OCTOBER 1961-SEPTEMBER 1972.

	Deer Cr.	Flynn Cr.	Needle Br.		
Month(s)	All years	All years	All years	Pre-logging[a]	Post-logging[b]
October	-0.119	-0.014	-0.221	0.829	0.586
November	-0.133	0.085	-0.060	-0.393	0.150
December	0.222	-0.174	-0.384	-0.382	0.292
January	-0.061	-0.139	-0.538	-0.804	-0.309
February	-0.136	-0.311	-0.269	0.645	0.686
March	0.209	0.304	-0.302	0.646	-0.144
April	0.571	0.399	-0.071	0.335	-0.256
May	0.415	0.423	0.589	0.558	0.277
June	-0.212	-0.210	-0.095	0.993**	0.720
July	-0.092	0.094	-0.158	0.335	0.465
August	-0.367	0.013	0.063	0.002	0.650
September	0.097	0.117	-0.262	0.264	0.718
Oct-Sept	0.214	0.006	-0.565	-0.906	0.336
Nov-Apr	0.195	-0.027	-0.574	-0.867	0.109
Jan-Apr	0.186	0.058	-0.711*	-0.654	-0.085
Mar-Apr	0.419	0.417	-0.249	0.669	-0.202
June-Sept	-0.173	-0.100	-0.135	0.551	0.755

[a] 1962-1965

[b] 1967-1972

* P <0.05

** P <0.01

In all three of these analyses the lack of consistency in the correlations was notable. Although one can attach plausible explanations to the statistically significant correlations, there were hardly more of them than might be expected due to chance in a series of that many analyses. Our conclusion is that there is no solid basis for a relationship between streamflow and abundance of coho salmon and cutthroat trout in these streams, a surprising result in the face of so much other evidence for such a relation. The small size of the streams involved and the resultant low numbers of juvenile fish may have reduced the power of the analysis, however.

In several western Oregon streams, Pearson et al. (1970) did a preliminary short-term study of the effects of streamflow on juvenile coho salmon during the summer low-flow season. From 1962 to 1965, they found a significant positive relationship between coho density (number/m^2) and minimum streamflow in McKay Creek, a tributary to the Tualatin River. They also found a significant positive relationship between mean water velocity in pools and coho density for 50 pools in five streams of the Nehalem River system. Preliminary data also indicated that streams with higher flows supported coho of larger sizes.

In streams in Maine, Havey and Davis (1970) found through multiple regression analysis of several environmental variables that rainfall in July and August, presumed to be an index of streamflow during the dry season, was the single most important factor influencing survival of Atlantic salmon from age 0+ to age 1+. Their multiple regression analysis was weakened, however, by a small sample size.

Wickett (1958) reviewed the effects of low water levels on adult migration and egg deposition by pink and chum salmon in British Columbia streams. Low flows result in excessive spawning density, leading to superimposition of redds and crowding of eggs. Adult migration is inhibited by low streamflow; other consequences include failure of egg deposition and increased predation on spawning fish crowded in shallow water.

The effects of streamflow on survival of pink and chum salmon in spawning beds were studied by McNeil (1966;1968) in streams in southeastern Alaska. Below normal streamflow, both in summer and winter, caused significant mortality of eggs and alevins in the gravel. In summer, low streamflow acted by causing low levels of dissolved oxygen in intragravel water. In winter, low streamflow led to freezing of eggs and alevins, especially in streams subject to greatly fluctuating flows. High streamflow during winter caused mortality by displacement of eggs and alevins from spawning gravel.

Studies have also been undertaken on the influence of streamflow on resident populations of salmonids. In Big Roche-a-Cri Creek, Wisconsin, brook trout biomass fluctuated greatly with streamflow. White (1975) found that from 1958 through 1966, biomass was significantly correlated with mean January-February discharge ($r = 0.867$).

Using data from Sagehen Creek, California, kindly provided by Dr. Richard Gard, we correlated mean monthly and seasonal discharge with mean annual biomass of brook, brown, and rainbow trout (Table 4). Brown trout biomass was best correlated with December flows and brook trout biomass showed the best correlation with February discharge. Neither of these was statistically significant, however. Rainbow trout biomass showed significant negative correlations with discharge in January, April, and June. Again, the total number of significant correlations among the 51 comparisons is very close to the number that would be expected by chance. However, the predominance of negative correlations for brook and rainbow trout and positive correlations for brown trout is in itself a significant result that deserves further analysis.

TABLE 4. CORRELATIONS BETWEEN MEAN MONTHLY DISCHARGE AND MEAN ANNUAL BIOMASS OF BROWN, BROOK, AND RAINBOW TROUT. SAGEHEN CREEK, CALIFORNIA, 1954-1961. DATA FROM DR. RICHARD GARD (PERSONAL COMMUNICATION).

Month(s)	Brown	Brook	Rainbow
January	0.040	-0.142	-0.806*
February	-0.174	-0.632	-0.495
March	-0.168	0.072	-0.449
April	0.067	0.023	-0.746*
May	0.183	-0.488	-0.595
June	0.123	-0.547	-0.727*
July	0.109	-0.494	-0.649
August	0.259	-0.408	-0.592
September	0.354	-0.275	-0.468
October	-0.416	-0.199	0.373
November	-0.050	-0.209	-0.127
December	0.514	0.146	0.147
Jan-Dec	0.208	-0.461	-0.294
Jan-June	0.137	-0.448	-0.305
March-June	0.151	-0.449	-0.339
March-April	0.164	-0.510	-0.454
July-Dec	0.426	-0.184	-0.080

* $P < 0.05$

Floods can have a very severe impact on salmonid and other fish populations. Wickett (1958) reported that floods are a major cause of mortality in pink and chum salmon streams in British Columbia and have often reduced the size of succeeding runs. The principal cause of mortality is scouring of eggs and alevins from the gravel. In Nile Creek, B.C., chum salmon survival was considerably reduced in years of severe floods. In 1945-46, there were no floods and the fry had a 3% survival rate. There were several severe floods in 1946-47 and 1947-48, with survival rates dropping to 0.44% and 0.38%, respectively. There was high water but no severe flooding in 1948-49 and fry survival increased to 6.0% (Neave and Wickett 1953).

In the Horokiwi stream, New Zealand, severe flooding occurred between May and October 1941. Based on studies over the previous year, Allen (1951) estimated the effects of these floods on the streambed, the benthic fauna, and the brown trout population. The bottom fauna was reduced to 40-50% of levels of the previous year. The estimated number of most age classes present in October 1941 was only 25-50% the number present of the same age in October 1940. Destruction of eggs by flooding represented 80-90%, compared to a negligible loss the year before. The reduction in bottom fauna resulted in a higher percentage of this food resource being required by the remaining reduced trout population just for maintenance. This reduction left a lower proportion of the food for growth. Thus the floods caused a reduction in the bottom fauna that limited the trout stock to a lower biomass and production. This effect occurred independently of the direct reduction in numbers of trout caused by the floods. Although the study terminated at that time, the limitation was presumed to be only temporary, with both benthos and trout populations returning to original levels in periods of normal rainfall.

In Valley Creek, Minnesota, four severe floods were recorded in 1965 and 1966. Two year classes of brook trout were nearly eliminated from the population. The older age groups were reduced as a result of changes in habitat caused by flooding (Elwood and Waters 1969). A later study showed that the brook trout population made a substantial recovery in 4-5 years. Standing crop increased from 498 fish/ha in 1966 to 10,882 fish/ha in 1969. Biomass increased from 2.5 g/m^2 in 1966 to 14.8 g/m^2 in 1970 (Hanson and Waters 1974), still somewhat lower than the average of about 25 g/m^2 from 1961 to 1965.

In Sagehen Creek, California, survival of spring-spawned rainbow trout fry increased in years following winter floods (Seegrist and Gard 1972). This increased survival of age-0 rainbow trout was presumed to be caused by reduced competition from young brook trout, a consequence of brook trout eggs being destroyed by flooding. When floods occurred in May, rainbow trout eggs were destroyed and survival of young brook trout was improved. Adult trout were less affected by flooding than were the young.

These studies illustrate the impacts that floods can have on salmonid populations. Generally, they affect the eggs and young, older fish being somewhat more resistant. The magnitude of the impact, however, can vary according to the severity of the storm, the particular species, the time of year, and the physical characteristics of the stream.

Habitat Quality

Salmonids are not uniformly distributed within a stream reach. If habitat preference or use can be defined for a species, the potential exists for prediction of spatial variation in abundance based on measurement of habitat quality. It may also be possible to relate temporal variability in abundance to seasonal changes in habitat caused by changing streamflow or other variables. A number of studies have attempted qualitative or quantitative description of habitat use by stream salmonids.

Juvenile coho salmon in their first summer prefer a pool environment. Emerging fry in Waddell Creek, California, initially utilized shallow gravel areas, particularly those near the stream margin (Shapovalov and Taft 1954). The youngest fry tended to school, but as the fish grew larger, these schools broke up and individuals took up territories, which they defended. The larger fry moved into deeper water and by July and August were mainly found in the deeper pools. Chapman (1962) further defined this territorial and aggressive behavior and related it to habitat utilization. Ruggles (1966) found that over twice as many fry remained in a pool-like environment than a riffle-like condition in stream channels in British Columbia. In Oregon streams, Nickelson and Reisenbichler (1977) described characteristics of prime habitat for juvenile coho salmon as having water depth of at least 30 cm, velocity of less than 30 cm/sec, a cobble substrate, and cover consisting of undercut banks and submerged roots.

In the South Fork system of the Salmon River, Idaho, juvenile summer chinook salmon rear primarily in the main stem. Platts and Partridge (1978) recently reported significant use of many tributaries as well. In these tributaries the juvenile salmon preferred high quality pools in the larger streams that had lower channel gradients and grassy streambanks. Yet 59% of all the salmon were found in stream reaches where less than 20% of the channel consisted of pools. This distribution was presumably the result of the fact that most of the juvenile chinook in the tributaries occupied stream reaches within 400 m of the main river, where there was naturally a low pool/riffle ratio.

In a north central Colorado stream, Stewart (1970) sampled 41 sections four times from June through September. He found mean depth and underwater, overhanging rock cover to be the most important variables determining the density of brook and rainbow trout larger than 18 cm. Undercut banks and areas of deep turbulent water seemed to be related to brook trout density, but not that of rainbow trout. He also presents useful data on spatial and temporal variation in biomass of the 41 sections, along with the physical data. Biomass of brook trout >18 cm varied from 0 to 63.9 g/m, rainbow trout 0 to 81.3 g/m, and combined trout 0 to 117.5 g/meter of stream (data on area not presented).

In Little Prickly Pear Creek, Montana, Lewis (1969) conducted a similar study involving 19 sections. He found that cover was the most important factor determining the density of brown trout. Increased stream velocity was associated with increases in density of both brown and rainbow trout per unit area of pool surface and per unit area of cover. The most stable trout populations occurred in deep, slow pools with extensive cover; brown trout showed greater stability than rainbow trout. Current velocity was the most important factor determining density of rainbow trout. Useful data on spatial variation in density are presented, but there is no information on biomass.

Use of habitat by steelhead trout was studied by Shapovalov and Taft (1954) in Waddell Creek, California. Young fry showed similar tendencies to coho fry, initially congregating in schools and later setting up territories. However, unlike coho, steelhead fry inhabited riffles in late summer rather than deep pools.

Dolly Varden fry in Hood Bay Creek, Alaska, were found in quiet water near stream banks and in small pools. The fry were usually inactive and found in or on the substrate, in contrast to the more aggressive coho fry, often found in the same habitat. The coho were actively swimming and feeding from the water surface (Blackett 1968).

Species interaction can have a strong influence on habitat utilization. Apparent preferences shown in the presence of a competing species may change if that species is absent, or if another is present, so care must be used in interpreting results from field studies of species interaction. Careful field observation coupled with experimental analysis is needed to define these interrelations.

Seasonal habitat preferences and behavior of juvenile coho salmon and steelhead trout were studied by Hartman (1965) in British Columbia. In spring and summer coho occupied pools and steelhead occupied riffles. Both were aggressive in defending their respective habitats. This behavior is similar to that observed in Waddell Creek, California, discussed earlier. In winter, however, both species inhabited pools. Low population numbers, low aggressiveness, and different microhabitat preferences were thought to be responsible for this coexistence.

Glova (1978) examined sympatric and allopatric populations of coho salmon and cutthroat trout in six British Columbia streams. In each, three habitats were defined in terms of stream velocity--pools (<8 cm/sec), glides (8-20 cm/sec), and riffles (>20 cm/sec). In sampling during 1973 in Bush and Holland creeks, where both species occurred, coho salmon dominated the salmonid biomass in pools, composing 53-91% of the combined biomass, compared to 9-47% made up by trout. In riffles trout were dominant, making up 63-88% of the combined total biomass. Glides were areas of intermediate biomass for both species, although coho also tended to dominate here, with 52-81% of total biomass. Above barrier falls, where they were found alone, cutthroat trout utilized pools more so than riffles, possibly due to the absence of coho. His analysis of diets suggested that coho were more specialized feeders, relying mainly on drifting foods, whereas cutthroat were more generalized, utilizing both drift and benthos. Glova (1978) noted that cutthroat emerged much later in the year than did coho salmon, into an environment that may already be saturated by coho fry. As a result of aggressive interaction with young coho, the trout would be largely restricted to riffle areas during summer and early fall, and this habitat type is usually less abundant than pools at this time. He concluded that production of sympatric trout may be limited by interspecific interaction, although total fish production may be greater in multi-species streams.

Glova (1978) also found that pools were more extensively utilized by the total fish species complex than were riffles. There was a strong negative correlation (r = -0.92) between the biomass of all fish species combined (coho salmon, cutthroat trout, and Coastrange sculpin, Cottus aleuticus) and mean stream velocity in Holland Creek during September. Based on behavioral studies he postulated that large pools would be less densely populated by salmonids than small ones, owing to competition near the heads of pools for incoming food and resultant low densities of fish in the downstream ends of the larger pools. In support of this hypothesis, he found a significant negative correlation (r = -0.40) between logarithms of salmonid biomass and pool surface area, based on data from a total of 37 pools in three streams.

In British Columbia, Bustard and Narver (1975b) found in experiments that overwintering coho salmon and cutthroat trout strongly preferred side-pools with overhanging bank cover to those without such cover. Given a choice between clean rubble substrate and silted rubble, they preferred the side-pools with clean rubble. In a natural stream studied during winter, age 1+ coho and steelhead were found mainly at greater depths and in deeper water than age 0 fish of either species. As stream temperature dropped below 9° C, coho and age 1+ steelhead occupied progressively deeper water and both species moved closer to cover (Bustard and Narver 1975a). Logs and upturned roots were the most commonly used cover. Steelhead were more closely associated with the substrate than were coho.

Habitat utilization by sympatric populations of coho and chinook salmon fry was studied by Lister and Genoe (1970) in the Big Qualicum River, British Columbia. At emergence, fry of both species were found along stream margins in association with streambank cover. As the young fish grew they moved into areas of faster velocity. Spatial segregation soon occurred between the two species because chinook fry emerged about one month earlier than coho fry and grew at a faster rate. As a result chinook preferred higher current velocities than did coho fry at a given date. Somewhat different results, involving more overlap of distribution and more interspecific interaction, were noted in an Oregon river where the two species emerged more nearly at the same time (Stein et al. 1972).

Diel variability in habitat preferences of juvenile chinook salmon and steelhead trout in Idaho streams was shown by Edmundson et al. (1968). Both species tended to move inshore at night to areas of quieter and shallower water than those occupied during the day. Steelhead used areas of faster velocity during the day than did chinook. Everest and Chapman (1972) found that most age 0 steelhead trout and chinook salmon in two Idaho streams lived in water velocities of less than 0.15 m/sec during summer. However, chinook occupied areas of finer substrate and deeper water than did steelhead. There is little interaction for living space between the two species because they spawn and emerge at different times; steelhead spawn in spring and chinook spawn in early fall. The larger juveniles tend to occupy deeper water, and the size differences resulting from these different spawning periods thus reduce competition for food and space between the two species (Chapman and Bjornn 1969).

Platts (1974) conducted an extensive study of fish habitats in 291 sites in 38 streams within the upper South Fork of the Salmon River system, Idaho. Geomorphic characteristics were an important determinant of population abundance. He found the highest fish population densities in channels having 30-50% pools. Total density of the fish populations was positively correlated with width and depth of the sampled streams. Rainbow trout and chinook salmon dominated the populations. Rainbow trout were predominantly found in riffles that were combined with shallow pools. Juvenile chinook were found most abundant in high quality pools.

In the Miramichi River, New Brunswick, Keenleyside (1962) studied habitats and feeding behavior of Atlantic salmon and brook trout. Salmon fry were most abundant in the upper reaches, where rapids and riffles were common. The fry were most abundant in fast water over substrate composed of small gravel and stones. Salmon parr (1-4 years old) were also more abundant in the upper sections of the river than the lower, but were found in deeper water and over larger substrate. Brook trout were found only in the upstream areas. Fry were most common in shallow slow-moving water along the margin. Older fish were found in deeper water that was often swift or turbulent. Keenleyside (1962) noticed feeding segregation between the species. Salmon fry and parr fed on benthic fauna and surface organisms, whereas trout fed almost exclusively on surface foods, possibly because they held positions further above the substrate than the salmon.

In the Indalsalven River, Sweden, brown trout and Atlantic salmon were found together (Lindroth 1955). The young trout (age 0+) occupied shallow water near the stream margin. The trout were territorial and aggressive, actively chasing salmon fry away from these areas. In Scottish streams, Mills (1969) found varying degrees of dominance between Atlantic salmon and brown trout. In some streams he found salmon fry and parr and juvenile trout living together in the same pools and riffles. All possible combinations were noted, from predominance of trout in some streams through to predominance of salmon in others.

Additional evidence that habitat quality is an important determinant of salmonid biomass comes from efforts to improve the quality of existing stream habitat. Although much of this work has gone unevaluated, a number of careful studies have shown population response to habitat development. Among the best documented is the work of Hunt (1971) at Lawrence Creek, Wisconsin. Habitat development in one 0.7 km section of the stream in 1964 increased permanent bank cover by 416% and pool area by 289%. As a result, total brook trout biomass increased from a mean of 59 kg in 1961-63 to 110 kg in 1965-67. In a follow-up study, Hunt (1976) found the mean total biomass in 1968-70 to have increased even further, to 165 kg (21.9 g/m^2).

One of the earliest studies on habitat development in the West was conducted by Tarzwell (1938) in two Arizona streams. In Horton Creek, small log dams, deflectors, and artificial bank cover were added to one section. A section of nearby Upper Tonto Creek was left unimproved as a control. From 1932 to 1937, 25,150 brook, brown, and rainbow trout were stocked in Horton Creek and 46,190 trout were stocked in Upper Tonto Creek.

A complete creel census was conducted in both streams. In 1936 and 1937, following improvement in Horton Creek, that stream yielded more trout to the angler, and a greater weight of trout per hectare than did Upper Tonto Creek, in spite of the much heavier stocking of the latter stream.

The effects of cover manipulation on trout abundance were studied by Boussu (1954) in Trout Creek, Montana. Four inventories were carried out before alteration of habitat (June, December, March, and June); three inventories were made after the alterations (September, December, and March). Rainbow and brook trout comprised about 98% of the salmonids, the remainder being a few brown trout. Brush cover totaling 14.4 m^2 was added to four sections of the stream having a total area of 263 m^2. Following the cover addition, total trout biomass in those sections increased from 1.13 kg to 4.04 kg (4.3 g/m^2 to 15.4 g/m^2). Trout biomass in three unaltered control sections increased only 22% (from 8.5 g/m^2 to 10.4 g/m^2). When 11.9 m^2 of natural brush cover were removed from two sections with an area of 108 m^2, trout biomass decreased from 3.83 kg to 2.28 kg (35.5 g/m^2 to 21.1 g/m^2). At the same time trout biomass in a control section increased 6% (38.1 g/m^2 to 40.5 g/m^2). The third treatment involved removal of 1.4 m^2 of undercut bank from two sections totaling 80 m^2. In this case biomass decreased from 0.68 kg to 0.45 kg (8.5 g/m^2 to 5.6 g/m^2), while biomass in a control area increased 20%, from 14.4 g/m^2 to 17.3 g/m^2. In each of the three treatments the response by legal-sized fish (>18 cm) to change in cover was greater than that of smaller fish. Another result of his work not explicitly presented was the finding of a very significant spatial variation in trout biomass. In the 13 sections used for the study the pre-alteration biomass averaged 16.4 g/m^2, but ranged from 0.11 to 46.7 g/m^2. Because the data are reported as averages for four sampling dates, actual variability was undoubtedly greater. It should also be noted that these data resulted from a single pass with an electroshocker through each section blocked with stop nets, rather than from a formal population estimate.

Thirteen dams, 12 deflectors, and several covers were constructed in a 411-meter section of Hayes Brook, Prince Edward Island, in 1959. In the following year, the number of age 0 brook trout increased to 526, compared with a 13-year pre-treatment mean of 482 (Saunders and Smith 1962). Numbers of older trout increased from a mean of 348 (1947-1959) to 611 in 1960.

Many of these studies have shown great variability in habitat preferences between species, at different times of the year, for different ages of fish, and in association with other species present. Knowledge of these preferences is an important concern in the design of a sampling program.

BIOLOGICAL FACTORS

Food Abundance

There has been an enormous amount of work done on food habits and feeding behavior of stream salmonids. However, very few of these studies bear directly on the matter at issue here: can differences in abundance or availability of food account for spatial or temporal variation in salmonid biomass in streams?

The question is complicated by difficulty in defining an appropriate measure of food availability--benthos, drift, or some combination. Very few studies have focused on these important issues. A reorientation of feeding studies is required before a definitive answer to the question of food limitation is possible. Our review will concentrate on the few studies relating food abundance to variation in salmonid abundance.

A starting point is to examine the significance of invertebrate drift. Drifting invertebrates represent a potential food source of considerable magnitude, but of variable availability. Of particular importance is a strong diel periodicity, most drift occurring during darkness. Other factors that may affect the rate of drift include water temperature, current velocity, stage of the life cycle, and population density (Waters 1969). Some studies (Mason and Chapman 1965; Elliot 1973; Gibson and Galbraith 1975) have shown greater fish standing crops in stream sections with greater incoming drift. Yet other studies have shown a significant part of the diet to be made up of non-drift benthic forms. For example, Warren et al. (1964) reported the greatest food consumption in stream sections with the least drift, possibly because of a much greater abundance of benthic fauna in these sections. Other work has shown little correlation between drift and diet. One such study was conducted by Mundie (1969) on coho salmon fry in British Columbia. In seeking an explanation for the lack of correlation he postulated diel and spatial variation in drift composition, and variation in fry behavior. It is clear that there is considerable variation in the degree to which drift is utilized as food by stream dwelling salmonids.

There is evidence that food can be a limiting factor for some populations of stream salmonids. One of the strongest cases was brought forward by Mason (1976). He found that food limited the stream production of juvenile coho salmon during the summer in Sandy Creek, B.C. Through supplemental feeding, the summer biomass was increased 6-7 fold compared with previous levels. However, there was no significant increase in the number of smolts the following spring. The estimate of smolt yield under natural conditions was 212 fish, and the February population estimate was 257±71 fish surviving from supplemental feeding the previous summer. Thus in this stream the winter carrying capacity appeared to be the ultimate limit to smolt production.

In the Horokiwi stream, New Zealand, Allen (1951) found evidence suggesting that the food supply of brown trout, primarily the benthic fauna, could play an important role in regulating the trout population. He found that an increase in trout abundance increased pressure on the food supply, decreasing the density of that supply. This resulted in a reduction in surplus food (the amount that could be used for growth and production). Consequently, there was a decrease in mean individual growth rate. This resulted in a feedback system that would tend to keep the population biomass relatively constant by changing growth rate in response to changes in population size.

In a later review, Allen (1969) discussed the role of the benthic fauna in regulating production of stream salmonids as a group. He suggests that fish production can be limited by the density of the bottom fauna, which in turn may be controlled by consumption by fish. This interaction provides a mechanism for stabilizing the salmonid production rate.

Ellis and Gowing (1957) examined bottom fauna and brown trout populations above and below a domestic sewage outfall into Houghton Creek, Michigan. Although the biomasses of trout were similar above and below, there were significant increases in the benthic fauna and condition of trout below the point of sewage input. They also noted that trout below the outfall relied less heavily on terrestrial foods, and concluded that trout growth was strongly influenced by the quantity and kinds of food consumed.

Symons (1971) experimented with effects of fluctuating food quantities on behavior and abundance of Atlantic salmon parr in a stream tank. He found that such fluctuations had little effect on the abundance of socially dominant parr. Socially subdominant fish, however, seemed more abundant where food was plentiful than where it was scarce. Thus total fish abundance was higher in channels where food was more abundant. Mason and Chapman (1965) studied behavior and abundance of juvenile coho salmon in two experimental stream channels. They found that one channel received about a third more volume in potential food organisms, and this was associated with about a two-thirds increase in total fish weight in that channel. However, there was no replication, and other causes may also have been involved.

Variation in food abundance was associated with spatial variation in abundance of cutthroat trout populations in the Oregon Cascades. One pair of open and shaded stream reaches was studied intensively for 4 years. Primary production and insect emergence were significantly greater in the open area compared to the forested section (Triska et al. 1980). Production, growth rate, and biomass of cutthroat trout were about twice as great in the open area (Hall et al. 1978). Murphy (1979) expanded the study to include nine pairs of open and forested sites, the openings being the results of earlier clearcuts. He found the same general relations to hold, including increased abundance of primary producers, predatory insects, and cutthroat trout in the open areas.

Predation

Although predation has been shown to cause some significant mortality in stream salmonids (Hunter 1959; Mills 1964; Tagmaz'yan 1971), there have been very few studies to support the position that variation in level of predation leads to ultimate variation in size of the salmonid population.

One of the few studies to combine stream population studies with predator manipulation was carried out over a number of years in New Brunswick. Elson (1962) reports investigations of predation on juvenile Atlantic salmon by mergansers and kingfishers from 1942 to 1953. In a sample of 117 merganser stomachs analyzed, an average of 42.1% of the number of items were salmon. These salmon comprised an average of 10.3% of the total fish numbers in the river, yielding a forage ratio of 4.1. Kingfishers also selectively fed on salmon and had a forage ratio of 3.1. Predator control was practiced from 1947 through 1950 and the abundance of mergansers and kingfishers was significantly reduced. Consumption of salmon by these two species of predators was estimated to have been reduced to about 10% of pre-control levels. Before control, smolt output ranged from approximately 1,000 to 5,000 each year. During predator control, output ranged from 14,000 to 24,000 smolts. Elson

(1962) concluded that predation by mergansers was a limiting factor on Atlantic salmon smolt production. Unfortunately, the study design was somewhat flawed by differing levels of stocking in the pre-control and control years, and by lack of data on adult returns.

One of the most detailed long-term studies on trout populations and predation has been carried out in Michigan on the North Branch of the Au Sable River (Alexander 1979). Estimates of population size of brook and brown trout were made in spring and fall each year from 1957 to 1967. Catch by anglers was determined from a statistically designed creel census in two sections of the river, one in which normal angling regulations prevailed and another in which angling was significantly restricted. Predators were collected for stomach analysis from 1960 to 1974. From these analyses Alexander concluded that the annual rate of mortality of both brook and brown trout was very high (average rates calculated by Chapman-Robson method for age groups 0-IV from his data in Tables 2-5: brook - 0.84 and 0.82; brown - 0.64 and 0.74, normal and special regulations respectively). Consumption by known predators (principally the American merganser, great blue heron, belted kingfisher, mink, otter, and large brown trout) accounted for a large fraction of this mortality; their consumption was estimated between 43 and 46% of annual production. Anglers took another 37 and 8% in the normal and restricted water respectively. Notwithstanding the sizeable mortality caused by predators, Alexander is of the opinion that reduction of their abundance, short of complete removal of all predators, would not have a significant impact on salmonid abundance, owing to a compensatory kill rate that would be demonstrated by the remaining predators. The fact that total annual mortality rates are similar for each age group in the two sections, in the face of much less angling "predation" in the special water, supports this view. More effort must be put into well-designed stream studies such as this one before a definitive conclusion on the significance of predation to population abundance of stream dwelling salmonids can be provided.

Movement and Migration

Nearly all salmonid species undergo varying degrees of movement in their lifetime. Some non-anadromous species undergo annual migrations within the same stream system for the purpose of spawning. Others remain in the same general area, undergoing local movements motivated by food, temperature, streamflow, or other factors. Movement and migration can be considered a form of temporal variability. The timing and magnitude of these movements need to be understood in order to know what age and size range of fish to expect from sampling at a particular time of the year. A comprehensive review of migratory strategies of freshwater fishes and their significance to fish production is provided by Northcote (1978).

Migrations of anadromous species are so conspicuous and generally well known that it seems unnecessary to include them in this review. One cautionary example is perhaps in order, however. Conventional wisdom for many years held that juvenile fall chinook salmon migrated to salt water shortly after emergence from the gravel, whereas juvenile spring chinook resided in fresh water for a full year before migrating to the ocean. More recent studies have indicated considerable variation from this pattern, both within and between stocks of fall and spring chinook (Reimers and Loeffel 1967; Reimers

1973; Schlucter and Lichatowich 1977). These results indicate the importance of careful studies of the migratory pattern in each stock of fish.

Most studies of resident salmonids have found their movement to be quite restricted, with the exception of some activity associated with spawning. In Kettle Creek, Pennsylvania, Watts et al. (1942) observed an upstream migration of brook trout into colder tributaries in late May and early June. Spawning took place in the fall, after which the trout moved downstream once again. Resident trout in this watershed, however, moved little between tributaries.

There have been several studies of the movements of resident brown trout. Solomon and Templeton (1976) studied a population in a 7.5 km section of a chalk stream in England, from which they recognized five life history stages with respect to movements and migration. The first was a downstream movement from hatching to nursery areas. Fish stayed in these areas for about 6 months. Then came a second movement further downstream to areas of adult growth, where the trout remained until they were about 15 months old. Following this was a period of very limited adult movement until maturation. Then came an upstream spawning migration followed by downstream movements after spawning.

In the Pine River, Michigan, Mense (1975) studied effects of varying brown trout densities on movement. Among fish >15 cm, he found no change in movement patterns in a comparison of densities of 209 and 87 trout/ha. He does not present data on biomass, but we have made a rough estimate of 3.8 and 3.3 g/m^2, based on his data for the two respective years. Both values for biomass are rather low, and the fact that the average size of fish was much larger in the year of lower density reduced the power of his test of the hypothesis.

In Convict Creek, California, Needham and Cramer (1943) found extensive downstream movement of brown trout during spring. The peak coincided with rising, but not maximum, streamflows, although flow was not felt to be a causative factor. Most migrants were sexually immature. The downstream migration may have been initiated by lack of adequate food and shelter in the upper reaches of the stream. Little migration of rainbow or cutthroat trout was noted.

Movement into and out of an intermittent tributary was shown to be an important feature in the life history of rainbow trout in Sagehen Creek, California. From 39 to 47% of the spawning adults used this tributary from 1972 to 1975. Two possible reasons were given for this high use of an intermittent stream while permanently flowing tributaries were used by only a small percentage of the spawning fish. Peak runoff from snow melt is much greater and occurs earlier in the year in the intermittent tributary. In addition, there is no competition from brook trout because they cannot spawn there in the fall owing to insufficient flow (Erman and Hawthorne 1976). The rainbow trout fry from this tributary showed a diel periodicity in downstream movement that differed between a dry and wet year. In 1973, the dry year, fry moved downstream mainly during the day. In 1974, when the tributary retained permanent flow, fry migrated downstream mainly at night. In that year many fry remained in the tributary throughout the summer (Erman and Leidy 1975).

In another population of rainbow trout, movement was not extensive. In Elder Creek, Oregon, Osborn (1967) made 755 observations of rainbow trout movement, based on recaptures of marked fish larger than 75 mm. Less than 4% of the fish had moved more than 91 m.

Several studies have indicated that resident cutthroat trout undergo relatively limited movements. In Gorge Creek, Alberta, Miller (1957) found that of 58 tagged fish recaptured, 32 (55%) were recovered in the same pool in which they were tagged. He concluded that most cutthroat in this stream had a home territory less than 18 m long. In Lookout Creek, Oregon, restricted home ranges were also found for cutthroat trout. Wyatt (1959) noticed no general downstream movement, but he did observe two periods of limited upstream movement. From October through January some trout made scattered visits to tributaries. Then from the end of March to early June there was a spawning migration, with a peak in April.

OTHER FACTORS

There are a number of other factors that may affect natural variation in abundance of salmonids. This section includes consideration of those factors that are worthy of mention but have not been studied in enough detail to warrant discussion in separate sections.

In the Pigeon River, Michigan, Benson (1953b) studied the effects of ground water on brook and brown trout populations. Spawning of brook trout occurred only in sections with considerable ground water seepage. Brown trout spawned in more widely scattered areas, but the greatest concentration of redds was located where ground water was abundant. In turn, these areas of greater spawning produced higher population estimates. In a later study in the same river system, Latta (1969) found that numbers of brook trout fry were directly correlated with ground water levels. He suggested that the relation would be stronger in lower reaches of streams than in headwaters.

Ice formation can have substantial effects on overwintering salmonid populations in high mountain streams or high latitudes. In Sagehen Creek, California, Needham and Jones (1959) noted that anchor ice, which forms underwater in riffle areas, is an important ecological factor in that it can raise the water level in pools and reduce streamflow over riffles. The breakup or melting of anchor ice can dislodge the benthic fauna, making more food available to trout. In British Columbia, Bustard (1974) found collapsing snow and subsurface ice to be two major causes of winter mortality in salmonids.

Beaver dams can significantly alter physical characteristics and carrying capacity of salmonid streams. In Sagehen Creek, California, the balance of abundance of brook, brown, and rainbow trout was shifted by the presence or absence of dams (Gard 1961).

Chemical properties of stream water may influence salmonid abundance and growth rate. In New South Wales, Lake (1957) examined brown and rainbow trout populations in 130 streams. He found a strong correlation between water chemistry and growth rate. Streams with the hardest water and highest pH had the most abundant bottom fauna and produced trout with the greatest length at a given age. Kennedy and Fitzmaurice (1971) examined over 40 streams and rivers in Ireland. They found the largest and fastest growing brown trout in streams having a high calcium content. The smallest and slowest growing ones were in lime deficient waters draining acid rocks. These results are supported by Thomas (1964) from rivers in west Wales. He found that the growth rate of brown trout in waters having a pH of 7 or more with a high ion and calcium content was greater than that in more acid waters. Brown trout populations in six streams of varying hardness in Pennsylvania were sampled by McFadden (1961a). There was no consistent difference in trout density between hard and soft water streams, yet brown trout growth rate was consistently greater in hard water streams. Fish of similar size had greater fecundity in hard water.

Stream gradient usually operates to limit distribution of salmonids, rather than abundance. However, in transitional areas, where two species are involved, consideration of gradient may help to explain variation in abundance. In the Clearwater River system, Idaho, Griffith (1972) found evidence suggesting that stream gradient may influence the relative abundance of brook and cutthroat trout in streams inhabited by both species. In some parts of Idaho cutthroat live in slow water (< 6 cm/sec) when not associated with brook trout, but they did not occupy this habitat in association with brook trout in Crystal Creek. Brook trout were found in the low gradient sections of Crystal Creek, whereas cutthroat were more abundant upstream in areas of higher gradient. The same distribution of the two species was also found in a tributary of the St. Joe River.

SECTION 5

MINIMIZING THE EFFECTS OF VARIABILITY IN IMPACT STUDIES

The temporal and spatial variability in populations of stream salmonids are clearly sufficient to mask very significant man-caused changes in these populations. This is especially true for damage done by non-point source pollutants. If we are to effectively monitor impacts of such perturbations, means must be found to minimize the effects of natural variability in detecting these effects. It now seems clear that the traditional watershed study design, with its long-term pre-treatment calibration and post-treatment evaluation, is not adequate for such analysis (Hall et al. 1978). After reviewing existing approaches to the problem, we present several interrelated ideas that may improve sensitivity of future studies.

HABITAT QUALITY RATING SYSTEMS

Models that quantitatively describe the quality of salmonid habitat promise to significantly reduce the amount of unexplained variability in population abundance. The principal stimulus for the development of many of these models has been concern about loss of water from streams caused by irrigation or other appropriation. Hence the focus has been on determination of minimum streamflow requirements and on changes in habitat quality and quantity with changing streamflow. A good review of the historical basis for this work is provided in proceedings of the Symposium on Instream Flow Needs (Orsborn and Allman 1976).

One of the early attempts to develop such a model was made by Wesche (1973), who combined hydrologic parameters, surface area, and available trout cover to define available habitat for brown trout. Continuation of this work extended the analysis to a cover rating system that provided a significant linear predictor of brown trout biomass in several stream systems (Wesche 1976).

Another early study was initiated by the Oregon Department of Fish and Wildlife, mentioned earlier. They began with an attempt to relate habitat quantity and quality to streamflow by manipulating flow in a natural stream channel through a diversion (Keeley and Nickelson 1974; Nickelson 1975). Though initial work was marred by technical difficulties in establishing the diversion, recent results have been quite promising. Two types of models are presently being developed. One describes the relation between stream habitat and rearing potential of salmonids during the low flow period. Another is designed to predict the amount of habitat for any value of streamflow (Nickelson and Reisenbichler 1977; Nickelson and Hafele 1978). Pool volume alone explained 93.5% of the variation in summer standing crop of juvenile coho salmon in 12 sections of three coastal streams. For cutthroat trout a habitat quality rating (HQR) is computed as a product of a cover value, velocity preference factor, and wetted area. The cover value is a combination of depth, escape cover, overhanging cover, turbulence, and velocity shelter. Two alternative formulations of the HQR explained 91 and 87% of the variation in cutthroat trout standing crop in 31 sections of six streams (Nickelson and Hafele 1978). A related HQR for steelhead trout, involving cover, depth and velocity, and wetted area, explained 79% of the variation in standing crop of juveniles in 23 sections of four streams. Further work is underway to validate these models.

A related approach has been taken in a follow-up of work done in Wyoming streams by Wesche (1976). Binns and Eiserman (1979) developed a habitat quality index for trout from analysis of 22 physical, chemical, and biological attributes in a sample of 36 streams. Using a multiple regression approach for selection of model attributes, they constructed an index (Model I) that produced an R^2 value of 0.955 for the initial 20 streams sampled. When this model was used to predict trout standing crop at 16 new stations, R^2 dropped to 0.594. A new model was developed for all 36 sites, based on only nine habitat attributes, all physical and chemical (late summer flow, annual flow variation, maximum stream temperature, and a food index and a cover index that are combinations of nitrate nitrogen, cover, eroding stream banks, substate, water velocity, and stream width). This new model (Model II) explained 97% of the variation in trout standing crop at the 36 sites ($R^2 = 0.966$). However, this analysis highlights a frequent misinterpretation of R^2 as a measure of reliability of the model (W.S. Overton, Department of Statistics, Oregon State Univ., personal communication). One value of standing crop is more than twice as large as the next largest (63.4[1] vs 28.4 g/m^2). This one point tends to inflate the value of R^2 by its large contribution to the sum of squares for standing crop. A more valid measure of the goodness of fit is the relative prediction error. The authors noted that no prediction was in error more than 5.5 g/m^2 and that an error of 5.4 g/m^2 at Sand Creek (the highest trout population) was within 9% of the measured value. However, the percent error at many stations with lower biomass was substantially higher than that, and averaged 32.4% for the 36 stations with Model I (range 0-179%) and 26.2% (range 0-157%) for Model II. Nonetheless, this approach is a very useful one that promises to increase the precision of impact evaluation.

The most extensive development of indices to habitat quality has been undertaken by the Cooperative Instream Flow Service Group of the U.S. Fish and Wildlife Service (Bovee and Cochnauer 1977, Bovee 1978). Their general approach has been to couple information on the state of several hydraulic parameters of the stream environment with a "probability of use" for a combination of these parameters. A weighted usable area is then calculated for each level of discharge for the various life history stages of each species of interest. This effort, focused on the effects of incremental losses of streamflow on reduction in quality and quantity of fish habitat, has been substantially influenced by the thinking of physical scientists, primarily hydrologists. The input from physical scientists has been a significant feature of the program and one that should be encouraged. Addition of the perspective of geomorphology (Platts 1974; Swanson and Lienkaemper 1978) could significantly improve the generality of the approach.

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[1] It is noteworthy that this estimate appears to be one of the largest ever reported for salmonid biomass in streams, especially in that it resulted from only a single pass through the study section.

PROCESS STUDIES

Understanding of the basic physical and biological processes that lead to biological production and eventually to fish production will provide a much sounder basis for assessment than has been available through the case history approach. One particularly relevant example is found in the analysis of temperature changes following logging in the Alsea Watershed Study (Brown 1967; Brown and Krygier 1970). By developing a model of the heating and cooling process in an undisturbed stream and quantifying each element in the energy budget, Brown was able to identify direct solar radiation as the primary source of warming in streams. This procedure allowed a prediction to be made of the potential impact before timber was cut, and thereby provided a basis for planning necessary buffer strips to minimize adverse effects caused by warming of stream water. The process study provided an energy budget approach that is general enough to be applied in most watersheds.

It is probably more feasible to carry out such studies of the physical processes in streams than those of the biological components. Additional work on physical process is now underway, for example, in suspended sediment and bedload transport (Beschta 1978; Beschta and Jackson 1979). Nonetheless, studies of biological process are essential to an understanding of variability in stream salmonid populations, and further emphasis must be placed there.

Though far from complete, the work in Mack Creek carried out under the Coniferous Forest Biome Study and mentioned earlier (Triska et al. 1980) provided some evidence of the validity of this approach. Knowledge of primary production, insect abundance, and trout production provided evidence that the higher trout biomass in streams flowing through clearcut areas was a real phenomenon rather than simply the result of movement of trout in response to preference for open areas. It also provided some evidence of at least one pathway through which the increase in trout production might have been achieved. Much more work will be necessary in many more systems, however, before models of biological processes will achieve the same level of understanding and predictability now enjoyed by models of physical processes in streams.

STREAM CLASSIFICATION

It seems clear that some sort of classification of streams and their watersheds will be an essential element of future impact assessment (W.S. Overton, pers. comm.). Classification has had a long history, especially in Europe, where it has been incorporated in management schemes (cf. Huet 1959).

However, the perspective of those involved in classification has often seemed to focus on differences rather than similarities of stream ecosystems, thus leading to unmanageable complexity in the system of classification (cf. Pennak 1971).

One of the approaches most adaptable to the present problem is that of Platts (1974). His classification is based on stream order and a small number of geomorphic characteristics and provides a manageable and quantifiable system. Application to a stream ecosystem encompassing 220 km of the South Fork of the Salmon River in Idaho provided significant explanation of variability in distribution and abundance of nine fish species.

A recent synthesis by Warren (1979) forwards a more inclusive classification scheme, based on a biogeoclimatic perspective. It takes the promising approach of classification based on capacity or potential of a system rather than its present state. This potential would be indexed solely by geomorphic characteristics of the stream habitat and the watershed system within which it is imbedded. The scheme thus avoids much of the complexity inherent in measuring both taxonomic and quantitative variability in biological components within and between stream ecosystems. Further development of this concept should provide a much more solid basis for impact assessment in the future.

IMPROVED STUDY DESIGN

Another source of improvement in efficiency of detection of impacts appears available through modifications in the way in which observational data are gathered. Field observations will probably always be the major basis for impact assessment. As a consequence, much of the body of experience and theory in the field of experimental design will not be directly applicable to such analysis. A sampling perspective is more appropriate, and Overton (1978) provides a useful discussion of three levels at which sampling questions can be addressed, along with general guidelines on study design.

Eberhardt (1978) provides a valuable review of the problems of appraising variability in population studies, one that should be required reading for anyone beginning a study to assess impacts of non-point source pollution. A related article (Eberhardt 1976) provides further detail, particularly on his suggestions for handling the "single-site problem" that is often a characteristic of impact assessment. He proposes substitution of repeated observations in time or space for true replication. The ratio of population density in the affected area to that in the "control" site(s) would be the measure of impact. He is cautious, indicating potential problems and suggesting the whole approach as a "pseudodesign." Nonetheless, these two papers are a very significant contribution to the topic under review here.

A number of different approaches to field observation are possible, and appropriate combinations may lead to more fruitful results than will a single approach. These possible approaches have been classified in two ways by Hall et al. (1978). In a review of effects of watershed perturbations on streams, they grouped studies according to whether they bracketed (before-after) or followed (post-) treatment. The other level of classification was based on whether detailed studies were made on one or very few streams (intensive) compared to less detailed work on many streams, including a wide range of habitat types (extensive). This two-level classification results in four categories, which are evaluated for efficiency and sensitivity of impact detection. An expanded listing of advantages and disadvantages of each type (Table 5) reveals that no one design is optimum. The extensive post-treatment approach does have a number of advantages over the classical watershed study (intensive before-after). The best approach appears to be a combination of extensive post-treatment analysis with carefully designed process studies carried out at one or more locations.

Pairing of treatment and control is proposed to improve sensitivity of detection (Hall et al. 1978). This procedure places an upstream control very close to a treatment area on each stream. It proved to be a sensitive design to investigate changes in both predator populations and their habitat in small clearcuts in the western Cascades in Oregon (Murphy 1979; Murphy and Hall MS.). By inclusion of watersheds that had been harvested up to 35 years earlier, it also provided some insight into the rate of change of physical and biological characteristics following treatment. This approach does have the limitation that it can detect only those effects that occur in the immediate stream reach affected by the treatment. It is relatively insensitive to downstream effects or those that accumulate over the larger watershed.

A modification that would provide some insight into effects on that scale would pair watersheds, treated and untreated. However, it would often be difficult to find untreated watersheds adjacent to treated areas, and such pairs would undoubtedly be more unlike than adjacent reaches of the same stream. Nonetheless Welch et al. (1977) used a variation on this approach to document effects of forestry and agriculture on streams in New Brunswick, examining a total of 34 watersheds, all smaller than about 1000 ha.

Erman et al. (1977) used an innovative form of this approach in a study of effects of clearcutting on invertebrate populations in Northern California streams. They sampled a total of 62 streams, all in small watersheds (< 800 ha). There were two objecives: to test effects of various widths of buffer strips in preventing changes in invertebrate populations, and to examine localized effects of point disturbances such as road-related landslides. For the latter purpose their design was to sample upstream of the landslide as a control, at the disturbance point, and downstream where no visual evidence of the disturbance remained.

To evaluate the role of bufferstrips, they used a design that employed two controls for each logged section, one upstream from the treatment and another in an adjacent untreated watershed. The hypothesis tested was that if effects occurred, the two control streams should be more similar than either control and the treated section. Various measures of similarity were compared and nonparametric ranking tests were used in the statistical analysis. They found significant effects on community composition in unbuffered streams and found no significant differences between controls and streams with wide bufferstrips (Newbold et al. in press).

TABLE 5. SUMMARY OF ADVANTAGES AND DISADVANTAGES OF THE FOUR MAJOR APPROACHES TO WATERSHED STREAM ANALYSIS.

A. Intensive Before-After (10-15 years; 5-7 years before and after treatment).

Advantages	Disadvantages
1) Possible to assess year-to-year variation and place size of impact in context of that variation.	1) No replication; results must be viewed as a case study.
2) Can assess short-term rate of recovery (ca. 5 years).	2) Results not necessarily applicable elsewhere (areas of different soils, geology, fish species, etc.)
3) No assumptions required about initial conditions.	3) Results vulnerable to unusual climatic events (e.g. high or low rainfall season(s) immediately following treatment).
4) Possible to monitor whole watershed impacts (provided substantial investment in facilities such as flow and sediment sampling wiers, fish traps).	4) Final results and management recommendations require exceptionally long time to formulate - up to 15 yrs after initial planning stage.
5) Long time frame provides format for extensive process studies.	5) Difficult to maintain intensity of investigation and continuity of investigators over such a long period.
	6) Must rely on outside agencies or firms to complete treatments as scheduled - considerable coordination required.

B. Extensive Before-After (2-4 years; 1 year before treatment, 1 year after).

Advantages	Disadvantages
1) Provides broader perspective across geographical area than (A).	1) Lack of long-term perspective--little opportunity to observe year-to-year variation.
2) Larger number of streams examined lessens danger of extreme case.	2) Able to assess only immediate results, which may not be representative of longer time sequence.
3) Increased generality of results allows some extrapolation to other areas.	3) Treatment vulnerable to unusual weather (if all treatments in same year).
4) Relatively short time to achieve results (3-4 years from planning stage).	4) Must rely on outside agency (see (A) above).

TABLE 5. (Continued.)

C. Intensive Post-Treatment (One Watershed--Paired Sites) (4-5 years, following treatment).

Advantages	Disadvantages
1) Shorter time for results than (A).	1) Provides no strict control--requires assumption that upstream control was identical to treated area prior to treatment.
2) Moderate ability to assess year-to-year variation.	2) "Control" most logically must be located upstream of treatment. Strong downstream trend in any feature would confound analysis.
3) Provides opportunity for moderate level of effort on process studies.	3) Provides no spatial perspective--results of limited application elsewhere.

D. Extensive Post-Treatment, 10-30 Watersheds (or more); all observations in 1-2 years (variable time after treatment).

Advantages	Disadvantages
1) Wide spatial perspective allows extrapolation to other areas.	1) No data available on pre-treatment conditions--forces assumption that control and treatment were identical (on average).
2) Long temporal perspective is possible--can assess recovery for as many years as past treatments have occurred.	2) Control predominately upstream.
3) Provides ability to assess interaction of physical setting and treatment effects (e.g. effects of sediment input at different stream gradients).	3) Total cost concentrated in very short period--requires extensive planning.
4) Requires least time of all four designs to get results--as little as 2 years.	4) Not as effective as (A) in assessing whole watershed effects.
5) Probably most economical of all four approaches per unit of information.	5) Methods used in early treatments may not be comparable to later ones.

Although much variability will undoubtedly remain in any study of natural populations in field situations, the ideas discussed above should help to resolve some of the uncertainty that has been present in past analyses. A good deal of ingenuity and insight will be needed in making the right choices of habitat parameters and in devising methods of quantifying them. Choosing the appropriate variables for watershed classification will likewise be a formidable task. Hopefully, however, some judicious combination of these approaches should make the task of assessing and controlling non-point source pollution a more effective and rational one.

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As part of a development of strategy for analysis of impacts of non-point source polluants on streams, we have searched the literature on population dynamics of stream salmonids. The following list is not exhaustive, but we have put emphasis on studies that report quantitative estimates of population size, and those that deal with spatial and temporal variability in such data. In addition we have included studies that may be useful in interpreting this variability. Some emphasis is placed on work on the west coast of North America, but many valuable contributions from other areas have also been included. The more important contributions in the following list are annotated; other reports of interest are listed only by title.

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Allen, K.R. 1951. The Horokiwi stream: a study of a trout population. New Zealand Mar. Dept. Fish. Bull. No. 10. 231 pp.

A classic study of the brown trout and benthic fauna in a New Zealand stream. Spatial variability in mean estimated trout biomass in six sections of the stream is presented for 1940 and 1941. Movements, mortality, production, growth, length-weight relationships, and angling effects are also analyzed. The bottom fauna is sampled in each section and total numbers and weights are estimated. The availability of these organisms in the stream is compared to the consumption by the trout and is expressed as forage ratios. The role of the food supply as a possible limiting factor in trout production is discussed. The effects of floods on the invertebrate fauna and trout population are also examined.

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A review of factors that can limit salmonid production in streams. In the egg stage in gravel, stream discharge and gravel permeability are critical. Predation, territoriality, and food availability are other stream factors of importance. The extent to which these factors can be limiting depends on the species, the amount of time spent in fresh water, the stream's physical characteristics, and climatic conditions.

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An encompassing study of coho salmon in the Alsea Watershed Study, in which one watershed was clearcut down to the streambank in 1966, another watershed was clearcut but buffer strips were left, and a third was left unlogged as a control. Fish traps enabled total counts to be made of upstream migrating adults and downstream migrating juveniles. Data on mean monthly biomass of juveniles are presented for the 1963-1968 year classes in each stream. Spawning migrations are analyzed in relation to streamflow. Sex ratios, redd location, fecundity, redd survival, and fry emergence are also discussed. Fry dispersal, colonization, behavior, and migration are also investigated. Population estimates, survival, growth, net production, and smolt yields are determined. No significant long-term effects of logging were noted in these populations. See also Chapman (1961; 1965) and Moring and Lantz (1975).

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A study of Atlantic salmon and brown trout populations in Shelligan Burn, Scotland from 1966 through 1968. Population size, growth rates, biomass, production, and yield data are presented. Variability in production is shown in three stream sections for the 1963-1968 year classes. Contributions of each year class to the total production for both species are discussed.

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A long-term study (1966-1975) of Atlantic salmon and brown trout populations in Shelligan Burn, Scotland. Mean biomass of each age group and total biomass of each species every year for the 10-year period are presented. Seasonal variability in growth rates, mean size and weight, and population density are investigated. Variability within each cohort through its lifetime is also discussed.

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A study of brown, rainbow, and brook trout populations in Little Prickly Pear Creek, Montana, during the summers of 1965 and 1966. Spatial variability is shown through data on biomass in 11 sections of the stream. Four of these sections have been altered due to adjacent railroad and highway construction. Major changes include straightening of the channel, loss of streambank cover, and changes in pool-riffle ratios. Comparisons are made between altered and unaltered sections in the same habitat zones in terms of physical stream characteristics and trout abundance.

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Gibson, R.J. 1973. The interrelationships of brook trout, *Salvelinus fontinalis* (Mitchill), and juvenile Atlantic salmon, *Salmo salar* L. Ph.D. thesis. Univ. Waterloo, Ontario.

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Glova, G.J. 1978. Pattern and mechanism of resource partitioning between stream populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki clarki*). Ph.D. thesis. Univ. British Columbia, Vancouver. 185 pp.

An investigation of sympatric and allopatric populations of coho salmon and cutthroat trout in six British Columbia streams from 1973 to 1976. Data are presented on biomass and fish length in pool, glide, and riffle habitats in each stream. Relationships between biomass and streamflow, pool area, and volume are examined. Spatial variability in salmonid density and biomass in three study sections in each of two streams is shown. Interactions between the two species are discussed in terms of abundances in different habitats. The importance of drift organisms in the diet of each species is investigated. Density and biomass of the sculpin (*Cottus aleuticus*) are estimated, and its relationships to the salmonids are studied.

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Four approaches to studying impacts of watershed management practices on streams are discussed. The long-term study is an intensive approach involving pre-treatment and post-treatment work on sites in the same stream. The extensive before-after approach is a short-term study involving sites in several streams. The intensive post-treatment analysis compares two adjacent sections of the same stream, one in a previously treated area and the other just upstream, over several years. The last technique is extensive post-treatment analysis, a short-term study involving comparisons between adjacent logged and forested stream sections in many watersheds. Advantages and disadvantages of each approach are discussed, as well as recommendations from statistical, practical, and economic viewpoints.

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Presents data on biomass of Atlantic salmon in this stream from 1960 through 1965. Biological and physical variables that could influence biomass and survival are studied. These factors include rainfall, streamflow, air temperature, water temperature, numerical standing crop, and biomass of other fish species in the stream. Regression analyses between these parameters and survival and biomass of age 0+ and I+ salmon are performed to determine those of greatest significance.

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Heiser, D.W. 1966. Age and growth of anadromous Dolly Varden char *Salvelinus malma* (Walbaum) in Eva Creek, Baranof Island, southeastern Alaska. Alaska Dept. Fish Game. Res. Rep. No. 5. 29 pp.

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Hobbs, D.F. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. New Zealand Mar. Dept. Fish. Bull. No. 6. 104 pp.

Holton, G.D. 1953. A trout population study on a small creek in Gallatin County, Montana. J. Wildl. Mgmt. 17:62-82.

Spatial variability in biomass of brook, brown, and rainbow trout is shown for four sections of Trout Creek, Montana in 1950 and 1951. This variability may be related to the relative distribution of the species, stream section width and depth, and pool-riffle ratios. Survival, growth, reproduction, and movements of these species are also examined. In addition, survival of planted brook trout is investigated.

Hoopes, R.L. 1975. Flooding as the result of Hurricane Agnes, and its effect on a native brook trout population in an infertile headwater stream in central Pennsylvania. Trans. Amer. Fish. Soc. 104:96-99.

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A study of brown trout and benthic invertebrate populations in two New Zealand streams. Seasonal trout population estimates from October 1964 through June 1966 are presented. Population density, growth, and food of the trout are analyzed. The availability of food and living space are discussed as potential limiting factors for the trout. The extent to which these factors are important with respect to size and age of the fish is also examined. In addition, data on biomass of the dominant benthic organisms in three study sections from 1964 through 1966 are presented.

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Horton, P.A., R.G. Baily, and S.I. Wilsdon. 1968. A comparative study of the bionomics of the salmonids of three Devon streams. Arch. Hydrobiol. 65:187-204.

Huet, M. 1959. Profiles and biology of Western European streams as related to fish management. Trans. Amer. Fish. Soc. 88:155-163.

Hunt, R.L. 1971. Responses of a brook trout population to habitat development in Lawrence Creek. Wisc. Dept. Nat. Resour. Tech. Bull. No. 48. 35 pp.

Hunt, R.L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wisc. Dept. Nat. Resour. Tech. Bull. No. 82. 28 pp.

Extensive data are presented on a long-term study of the brook trout population in this Wisconsin stream from 1960 through 1970. Production is given for the entire population and by age group for four stream study sections. Temporal variability in biomass is also shown by age group for April and September. Comparison is made between production in one section that underwent habitat development and production in the other sections. A discussion of compensatory mechanisms in growth and survival of each age group that keep the total production at a relatively stable level is also included.

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Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Bd. Can. 16:835-886.

A comprehensive study of factors affecting survival and production of pink and chum salmon in Hooknose Creek, British Columbia, from 1947 through 1956. Effects of temperature, stream discharge, sex ratio, population density, and predation on these populations are analyzed. Data on the number of predators (coho salmon and sculpin) as well as weir counts of pink and chum salmon fry and percent predation are given for each year of the study.

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Keeley, P.L., and T.E. Nickelson. 1974. Streamflow requirements of salmonids. Ore. Wildl. Comm. Ann. Prog. Rep. AFS-62-3. 18 pp.

Keenleyside, M.H.A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. J. Fish. Res. Bd. Can. 19:625-634.

Kennedy, M., and P. Fitzmaurice. 1971. Growth and food of brown trout *Salmo trutta* (L.) in Irish waters. Proc. Roy. Irish Acad. 71, Sect. B. (18):269-352.

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Koski, K V. 1975. The survival and fitness of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Ph.D. thesis. Univ. of Washington, Seattle. 211 pp.

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A comprehensive survey of 100 streams containing brown and/or rainbow trout. These are divided into three general categories with corresponding differences in mean pH, mean temperatures, bottom fauna production, and trout growth. Analysis of angling effects on the trout populations is also undertaken.

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Latta, W.C. 1969. Some factors affecting survival of young-of-the-year brook trout, *Salvelinus fontinalis* (Mitchill), in streams. Pp. 229-242 *in* T.G. Northcote (ed.), Symposium on salmon and trout in streams; H.R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

A study of age 0 brook trout from the Pigeon River, Michigan, in 1962, 1964, and 1965. Magnitude and periodicity of mortality are discussed in a brief review of other studies. Mortality from starvation, in relation to water temperature, is investigated in stream aquaria. Relationships between levels of groundwater and abundance of fry are also examined. The importance of groundwater levels in regulating the carrying capacity of the stream is discussed.

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A study of brown and rainbow trout populations in pools of Little Prickly Pear Creek, Montana, in the summers of 1965 and 1966. The importance of surface area, volume, depth, streamflow, and cover in accounting for the variation in population numbers is examined. Combinations of these factors are also considered as well as differential responses of the two species. Cover is discussed in terms of protection and photonegative response; streamflow is analyzed in terms of space-food relationships.

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Lindsay, R.B. 1974. Distribution and survival of coho salmon fry after emigration from natal streams. M.S. thesis. Oregon State Univ., Corvallis. 41 pp.

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Lorz, H.W. 1974. Ecology and management of brown trout in Little Deschutes River. Ore. Wildl. Comm. Fish. Res. Rep. No. 8. 49 pp.

Lowry, G.R. 1964. Net production, movement, and food of cutthroat trout (*Salmo clarki* Richardson) in three Oregon coastal streams. M.S. thesis. Oregon State Univ., Corvallis. 72 pp.

A study of cutthroat trout populations in the streams of the Alsea Watershed Study in 1962 and 1963. Population size, growth rate, and net production estimates are made. Data on monthly biomass for the 1959-1962 year classes are presented. Magnitude and timing of upstream adult and downstream kelt and smolt migrations are investigated. Trout food habits are studied during the time of emergence and early growth of coho salmon fry to determine the extent of predation. Seasonal variation in kind and quantity of food consumed is also examined. Much of the information is published in Lowry (1965 and 1966).

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Lowry, G.R. 1966. Production and food of cutthroat trout in three Oregon coastal streams. J. Wildl. Mgmt. 30:754-767.

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Manion, P.J. 1977. Downstream movement of fish in a tributary of southern Lake Superior. Progr. Fish-Cult. 39:14-16.

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Mason, J.C. 1974. Movements of fish populations in Lymn Creek, Vancouver Island: A summary of weir operations during 1971 and 1972 including comments on specific life histories. Can. Fish. Mar. Serv. Tech. Rep. 483. 35 pp.

Mason, J.C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (*Oncorhynchus kisutch*) fry. J. Fish. Res. Bd. Can. 32:2542-2547.

Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Mgmt. 40:775-788.

An important study on the role of food as a limiting factor in juvenile coho salmon production in a small British Columbia stream. Supplemental feeding resulted in a six-fold increase in the stream carrying capacity. Effects of this feeding on survival, growth, and pre-winter lipid reserve are also examined. However, there were no effects on the smolt yield the following spring. Attempts to increase winter carrying capacity by installing artificial refuges were ineffective. Complex winter behavior patterns may be responsible in limiting the population size.

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A study of juvenile coho salmon behavior in artificial stream channels. Aggressive behavior is observed within 1 week of emergence and is investigated for 5 months. Territorial defense, threat, and chasing are examined. Distribution in pool and riffle areas is studied. The effects of different times of emergence on fish size and territoriality are also examined. Environmental rearing capacity is discussed in terms of food and stream area.

McDonald, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. J. Fish. Res. Bd. Can. 17:655-676.

McFadden, J.T. 1961a. An ecological comparison of six brown trout (*Salmo trutta*) populations. Ph.D. thesis. Pennsylvania State Univ. 91 pp.

McFadden, J.T. 1961b. A population study of the brook trout, *Salvelinus fontinalis*. Wildl. Monogr. No. 7. 73 pp.

A comprehensive study of the brook trout population in Lawrence Creek, Wisconsin, from 1953 through 1957. Data are presented on population estimates, lengths, age structure, density, biomass, and natural mortality in each of four study sections for each age group of trout. Length-fecundity relationships are also examined. Angling intensity is investigated by means of a complete creel census each year. Data obtained include number of fishing trips, number, sex, size, and weight of trout caught and exploitation rates. Angler mortality is compared to natural mortality of the trout, and management options are discussed as means of keeping an adequate recruitment to the population.

McFadden, J.T. 1969. Dynamics and regulation of salmonid populations in streams. Pp. 313-329 *in* T.G. Northcote (ed.), Symposium on salmon and trout in streams; H.R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

McFadden, J.T., G.R. Alexander, and D.S. Shetter. 1967. Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. J. Fish. Res. Bd. Can. 24:1425-1459.

McKernan, D.L., D.R. Johnson, and J.I. Hodges. 1950. Some factors influencing the trends of salmon populations in Oregon. Trans. N. Amer. Wildl. Conf. 15:427-449.

One of the earlier studies attempting to explain fluctuations in salmon population levels in Oregon. Columbia River chinook salmon catch data are presented from 1866 through 1948 and coho salmon catch data from coastal rivers are presented from 1923 to 1948. Pollution, changes in angling regulations, hatcheries, logging, streamflow, and salinity are analyzed as potential factors responsible for the observed fluctuations. In addition, the effects of the fishery, indicated by marking experiments, fishing intensity, and economic trends, are examined.

McNeil, W.J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. Fish. Bull. 65:495-523.

McNeil, W.J. 1968. Effect of streamflow on survival of pink and chum salmon in spawning beds. Pp. 96-114 in Proc. Forum on the relation between logging and salmon. Feb. 8-9, 1968. Alaska Distr., Amer. Inst. Fish. Res. Biol., Juneau.

McNeil, W.J. 1969. Survival of pink and chum salmon eggs and alevins. Pp. 101-117 in T.G. Northcote (ed.), Symposium on salmon and trout in streams, H.R. MacMillan Lectures in Fisheries. Univ. British Columbia.

Reviews a long-term study of freshwater survival from 1940 through 1965. Also discussed are a dome-shaped production curve, density-independent mortality from droughts, floods, and freezing temperatures, and density-dependent mortality from redd superimposition.

Mense, J.B. 1970. Relation of density to brown trout movement in a Michigan stream. Ph.D. thesis. Mich. State Univ. 82 pp.

Mense, J.B. 1975. Relation of density to brown trout movement in a Michigan stream. Trans. Amer. Fish. Soc. 104:688-695.

Merrell, T.R. 1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. Pp. 59-72 in N.J. Wilimovsky (ed.), Symposium on pink salmon; H.R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

Presents data on number of spawners, egg deposition, number of seaward migrating fry, and freshwater survival from 1940 through 1959. Differences in magnitude and timing between odd-year runs and even-year runs are examined. Preliminary data in the last year of the study seem to indicate survival is related to stream gradient. There also seems to be a relationship between size of the run and section of the stream used for spawning.

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Miller, W.H. 1971. Factors influencing migration of chinook salmon fry (Oncorhynchus tshawytscha) in the Salmon River, Idaho. Ph.D. thesis. Univ. Idaho, Moscow.

Mills, D.H. 1964. The ecology of the young stages of the Atlantic salmon in the River Bran, Ross-Shire. Freshw. Salmon Fish. Res. Edinburgh. No. 32. 58 pp.

Mills, D.H. 1969. The survival of juvenile Atlantic salmon and brown trout in some Scottish streams. Pp. 217-228 in T.G. Northcote (ed.),

Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

Moring, J.R. 1975. The Alsea Watershed Study: Effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part II - Changes in environmental conditions. Ore. Dept. Fish Wildl., Fish. Res. Rep. No. 9. 39 pp.

Moring, J.R., and R.L. Lantz. 1975. The Alsea Watershed Study: Effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part I - Biological studies. Ore. Dept. Fish Wildl., Fish. Res. Rep. No. 9. 66 pp.

A summary report, incorporating data from a number of earlier publications from the study. Three small tributaries were studied, one clearcut down to the streambank, one clearcut with buffer strips left, and the third left uncut as a control, for 15 years. The pre-logging period was 1959 to 1965 and the post-logging period was 1967 to 1973. Biological studies concentrate mainly on coho salmon and cutthroat trout, the dominant species in the streams. For adults, data include numbers, timing of migration, size, sex ratio, and fecundity. Data on juveniles include emergence, growth, biomass, production, mortality, and downstream migration. Effects of logging are reported.

Mortensen, E. 1977. Population, survival, growth and production of trout *Salmo trutta* in a small Danish stream. Oikos 28:9-15.

Population dynamics of brown trout in a small Danish stream were examined from 1973 through 1975. Biomass of the 1971-1975 year classes is investigated. Population size, production, mortality, length-weight relationships, and smolt yield are also discussed.

Mortensen, E. 1978. The population dynamics and production of trout (*Salmo trutta* L.) in a small Danish stream. Pp. 151-160 *in* J.R. Moring (ed.), Proc. wild trout - catchable trout symp. Ore. Dept. Fish Wildl., Res. Devel. Sect., Portland.

Population size, survival, growth, biomass, and production of brown trout were studied in three sections of a small Danish stream from 1974 through 1976. Variability in age group composition and biomass between the three sections is shown. Density-dependent fry mortality, density-independent mortality of older fish, and variability in production-biomass ratios between age groups are also analyzed.

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Magnitude and timing of upstream adult and downstream kelt and smolt migrations in this river are examined for both species. Marking experiments are used to determine movements, utilization, and survival. Marine survival is determined from commercial catch and escapement of marked fish.

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An extensive survey of the major streams in Newfoundland, including description, location, and certain morphometric, edaphic, climatic, and biotic characteristics. Morphometric factors examined include watershed shape, elevation, gradient, vegetational cover, runoff, and discharge. Edaphic factors include surface geology, total dissolved solids, micronutrients, acidity, conductivity, and hardness. Climatic factors examined are air temperature and precipitation. Competition, predation, fecundity, emigration, survival, and disease are the biotic factors investigated. Both fish and aquatic invertebrate populations are studied. Native salmonid species are Atlantic salmon, brook trout, and Arctic char. Pink salmon, rainbow trout, and brown trout have been introduced. In addition, the sport fishery for Atlantic salmon is examined.

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The initial data from a long-term study of the effects of logging on the aquatic resources of a British Columbia watershed. The study is divided into pre-logging (1970-1974), logging (1975-1979), and post-logging (after 1979) periods. In particular sampling is

conducted on sections of upper and lower Carnation Creek, "C" tributary, "1600" tributary, and Useless, Frederick, Ritherdon, and South Pachena creeks. This report contains data on population estimates, density, late summer biomass, growth, length-weight relationships, and condition of both resident and anadromous salmonids. The primary species include coho and chum salmon, and rainbow, steelhead, and cutthroat trout. Data are updated for every year through 1977 by Andersen and Narver (1975) and Andersen (1978).

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A review of some chemical, physical, and biological factors that affect salmon populations in British Columbia streams. Chemical factors include dissolved oxygen and pH. Important physical factors are bottom type, particularly on spawning grounds, obstructions, streamflow, including floods, and water temperature. Predation, interspecific and intraspecific competition, and disease are important biological factors discussed. Relationships between precipitation and adult returns two years later are also analyzed.

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A study of the brown trout populations in two sections of this stream from 1939 to 1944, one closed and the other open to angling. Reproduction, survival, seasonal weight changes, and density are analyzed in both sections. The effects of angling on these parameters are shown. The possibility of stocking the stream with more trout is discussed as a method to offset angling pressure.

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A study of summer juvenile coho salmon populations in 19 streams in four Oregon river systems from 1962 through 1966. Relationships between minimum streamflow and coho density are examined. Mean pool velocity and fish density in pools also seem to be related. Effects of streamflow on fish size and incidence of disease are investigated. Fish numbers and size are related to the rearing capacity of a stream. Shade, cover, temperature, bottom composition, stream size, competition, and food production can also affect coho rearing capacity.

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An extensive study from 1970 to 1972 on conditions influencing salmonid populations in 291 stream sites in the upper South Fork of the Salmon River watershed, Idaho. Physical and hydrologic parameters examined include climate, geological processes and types, stream channel width, depth, gradient, and order, elevation, pool-riffle ratios, and streambank vegetation and stability. Effects of these factors on the salmonid populations are analyzed. The salmonid species present include rainbow, steelhead, and brook trout, Dolly Varden, chinook salmon, and mountain whitefish.

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A comprehensive long-term study of wild and hatchery coho salmon populations from 1938 to 1953. Magnitude and timing of upstream adult and jack migrations are investigated. Numbers, lengths, and timing of both hatchery and wild smolt migrations are studied.

For the hatchery-reared fish, fecundity, freshwater survival, marine survival, and total survival are evaluated for various rearing period durations. For wild fish, fecundity and survival are also investigated. Comparisons of these data, as well as contributions to the commercial fishery, are made. In addition, estimates for optimum wild escapement are presented.

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(*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dept. Fish Game Bull. No. 98. 375 pp.

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Streamflow is the primary factor investigated in relation to pink and chum salmon production in British Columbia streams. Effects of low flow on adult migration and egg deposition are discussed. Negative impacts of floods on populations are also examined. Effects of streamflow on incubation stages and the survival of deposited eggs are analyzed. Another factor discussed is spawner density, in relation to egg density and gravel permeability.

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A weir was set up on this Oregon tributary to the lower Columbia River. Counts of migrating coho and chinook salmon were made from 1955 through 1961. Timing of migration, adult-jack relationships, sex ratios, fecundity, and freshwater survival of wild fish are examined. Survival of hatchery-released fish in this stream is also analyzed. Preliminary data indicate that commercial gill-net catches in the lower Columbia River are related to discharge in Gnat Creek two years earlier.

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APPENDIX

This appendix is a compilation of examples of the best data available on temporal and spatial variation in populations of stream salmonids (reprinted here with permission of the copyright owners and publishers).

The tables are arranged geographically--north to south, west to east. A dash in lieu of data indicates "not sampled."

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Pacific Biological Station, Canada Department of Fisheries and Oceans, Nanaimo, British Columbia: Table A-4.

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Oregon Department of Fish and Wildlife: Table A-7.

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Institute of Animal Resource Ecology, University of British Columbia: Table A-1.

Washington State Department of Fisheries: Table A-6.

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Wisconsin Academy of Science, Arts, and Letters: Table A-25.

Wisconsin Department of Natural Resources: Tables A-26, A-27.

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Dr. Richard Gard: Tables A-16, A-17, A-18.

Dr. Gordon Glove: Table A-5.

Mr. Gerald Lowry: Table A-14.

TABLE A-1. POTENTIAL EGG DEPOSITION AND FRESHWATER SURVIVAL OF PINK SALMON, SASHIN CREEK, ALASKA, 1940-1959 (FROM MERRELL 1962).

Brood Year	Potential Egg Deposition[a]	Number of Migrating Fry	Freshwater Survival (%)
1940	52,858,000	3,402,830	6.4
1941	88,678,000	1,024,364	1.2
1942	81,502,000	674,672	0.8
1943	14,980,000	227,673	1.5
1944	3,904,000	104,113	2.7
1945	5,062,000	41,900	0.8
1946	736,000	1,168	0.2
1947	1,330,000	26,454	2.0
1948	516,000	9,016	1.7
1949	4,800,000	176,025	3.7
1950	86,000	(50 killed)	0.1
1951	4,062,000	379,585	9.3
1952	run destroyed	0	-
1953	1,284,000	90,219	7.0
1954	12,000	576	4.8
1955	10,286,000	1,232,872	12.2
1956	1,018,000	5,043	0.5
1957	2,587,758	588,976	22.8
1958	174,000	10,577	6.1
1959	40,379,327	5,332,468	13.2

[a] Based on 2,000 eggs per female except when actual fecundity was calculated in 1957 (1,986 eggs) and 1959 (2,021 eggs).

TABLE A-2. WEIR COUNTS OF COHO SALMON FRY AND SMOLTS, SASHIN CREEK, ALASKA, 1956-1968 (FROM CRONE AND BOND 1976).

Year	Total Count	
	Fry	Smolts
1956	-	928
1957	373	1,961
1958	2,854	1,015
1959	218	1,587
1960	9,923	1,258
1961	2,699	2,489
1962	1,209	2,865
1963	1,236	1,599
1964	44,023	334[a]
1965[b]	12,000	-
1967[b]	10,000	1,400
1968	1,665	1,440

[a] Partial count.

[b] Weir not functional. Counts are estimates from fyke net sampling. Weir damaged in 1966 - no sampling conducted.

TABLE A-3. WEIR COUNTS OF DOWNSTREAM MIGRATING PINK AND CHUM SALMON FRY, HOOKNOSE CREEK, BRITISH COLUMBIA, 1947-1956 (FROM HUNTER 1959).

Brood Year	Pink	Chum	Total
1947	33,349	108,746	142,095
1948	64,312	77,539	141,851
1949	54,061	44,463	98,524
1950	234,396	431,399	665,795
1951	242,993	269,701	512,694
1952	1,227,025	182,200	1,409,225
1953	204,250	984,504	1,188,754
1954	907,458	353,761	1,261,219
1955	86,256	49,443	135,699
1956	454,148	69,830	523,978

TABLE A-4. BIOMASS (g/m^2 IN LATE SUMMER) OF COHO SALMON AND RAINBOW AND CUTTHROAT TROUT IN STREAMS IN THE VICINITY OF THE CARNATION CREEK WATERSHED, BRITISH COLUMBIA, 1970-1977 (FROM NARVER AND ANDERSON 1974; ANDERSON AND NARVER 1975; AND ANDERSON 1978).

	Lower Carnation Cr.		Upper Carnation Cr.	Trib "C"	Trib "1600"		Useless Cr.		Frederick Cr.		Ritherdon Cr.	S. Pachena Cr.	
Year	Coho	Rainbow	Cutthroat	Cutthroat	Coho	Cutthroat	Coho	Cutthroat	Coho	Rainbow	Cutthroat	Coho	Rainbow
1970	2.72	1.21	-	-									
1971	1.89	0.92	3.46	-	-	-	-	-	1.06	0.0	5.36	1.87	1.24
1972	1.47	0.43	2.90	4.79	4.88	1.93	0.84	1.64	1.54	0.33	4.50	1.31	1.11
1973	1.46	0.59	3.97	5.64	2.45	1.97	0.19	1.66	-	-	3.07	0.74	0.42
1974	1.59	0.49	1.94	3.45	2.84	0.95	0.28	2.39	0.44	0.04	3.31	0.59	0.18
1975	1.64	0.44	1.66	3.71	4.19	0.39	0.70	2.01	1.36	0.07	2.84	1.85	0.23
1976	1.23	0.30	1.94	2.77	2.75	0.25	0.38	0.67	0.66	0.02	1.40	0.82	0.17
1977	1.62	0.32	1.08	2.47	-	-	0.53	0.85	0.95	0.09	1.38	1.40	0.37

TABLE A-5. BIOMASS (g/m^2) OF CUTTHROAT TROUT, COHO SALMON, AND SCULPIN IN DIFFERENT HABITATS OF SIX BRITISH COLUMBIA STREAMS, 1973-1976 (FROM GLOVA 1978 AND GLOVA PERS. COMM.).

Stream	Date	Habitat[a]	Mean Area (m^2)	Mean Depth (cm)	Biomass			
					Trout	Coho	Sculpin[b]	Total
Bush Creek	Sept-Oct 1973	Pools	42	16	0.3	3.3	3.2	6.8
		Glides	21	11	1.1	2.4	2.5	6.0
		Riffles	17	7	0.5	0.4	2.0	2.9
	Sept-Oct 1974	Pools	32	22	0.5	3.6	3.1	7.2
		Glides	32	12	0.5	2.0	3.5	6.0
		Riffles	22	11	1.2	1.2	1.7	4.1
	Sept-Oct 1975	Pools	45	38	0.7	2.0	3.9	6.6
		Glides	30	12	0.5	1.9	3.3	5.7
		Riffles	33	9	0.4	0.4	1.9	2.7
Holland Creek	Sept-Oct 1973	Pools	28	21	1.0	1.9	3.9	6.8
		Glides	29	11	0.8	0.8	2.0	3.6
		Riffles	13	8	1.1	0.2	1.4	2.7
	Sept-Oct 1974	Pools	23	34	0.6	1.3	4.6	6.5
		Glides	22	27	0.8	1.8	1.7	4.3
		Riffles	18	11	0.6	0.4	1.5	2.5
	Sept-Oct 1975	Pools	31	37	0.5	1.4	5.1	7.0
		Glides	49	18	0.2	0.9	2.8	3.9
		Riffles	35	12	0.3	0.2	2.3	2.8
Ayum Creek	Oct 1975	Pools	40	41	1.2	2.1	5.7	9.0
		Glides	53	19	1.0	1.9	2.2	5.1
		Riffles	56	15	0.8	0.7	0.5	2.0
Shawnigan Creek	Oct 1975	Pools	71	31	1.3	0.0	0.1	1.4
		Glides	39	13	1.2	0.0	0.1	1.3
		Riffles	25	9	1.0	0.0	0.0	1.0
French Creek above barrier falls	Sept 1976	Pools	56	31	2.5	0.0	0.0	2.5
		Glides	54	16	1.7	0.0	0.0	1.7
		Riffles	20	11	1.2	0.0	0.0	1.2
Bings Creek above barrier falls	Oct 1976	Pools	46	36	5.4	0.0	0.0	5.4
		Glides	50	18	2.6	0.0	0.0	2.6
		Riffles	27	11	2.1	0.0	0.0	2.1

[a] Determined by water velocities - pool (<8 cm/sec), glide (8-20 cm/sec), and riffle (>20 cm/sec).

[b] Mainly Cottus aleuticus.

TABLE A-6. ESCAPEMENT, POTENTIAL EGG DEPOSITION, AND FRESHWATER SURVIVAL OF WILD COHO SALMON, MINTER CREEK, WASHINGTON, 1938-1953 (FROM SALO AND BAYLIFF 1958).

Brood Year	Females Released Upstream	Egg Potential	Smolt Count	Freshwater Survival (%)
1938	967	2,657,316	35,452	1.33
1940	1,393	4,577,398	32,085	0.70
1942	786	1,873,038	31,893	1.70
1943	906	2,092,860	23,177	1.11
1944	500	1,376,500	30,408	2.21
1946	500	1,097,000	41,848	3.81
1948	98	186,200	17,839	9.58
1949	114	287,964	27,781	9.65
1951	411	1,086,684	22,545	2.07
1952	753	1,929,186	31,363	1.63
1953	491	1,150,413	18,620	1.62

TABLE A-7. COUNTS OF SPAWNING COHO SALMON AND SMOLTS AT DOWNSTREAM WEIR ON GNAT CREEK, OREGON, 1954-1959 (FROM WILLIS 1962).

Brood Year	Female Spawners	Smolt Count
1955	26	2,996
1956	29	1,847
1957	67	1,013
1958	40	1,061
1959	45	3,226

TABLE A-8. ESCAPEMENT, POTENTIAL EGG DEPOSITION, AND FRESHWATER SURVIVAL OF COHO SALMON, DEER CREEK, OREGON, 1959-1971 (FROM KNIGHT 1980).

Brood Year	Female Escapement	Egg Potential[a]	Smolt Count	Freshwater Survival (%)
1959	21	43,197	1,917	4.44
1960	19	44,156	2,210	5.00
1961	28	67,620	2,775	4.10
1962	18	42,030	2,082	4.95
1963	27	62,964	2,368	3.76
1964	44	104,940	1,836	1.75
1965	24	55,176	2,245	4.07
1966	56	141,798	2,461	1.74
1967	23	52,815	2,160	4.09
1968	39	80,301	1,484	1.85
1969	8	15,484	738	4.77
1970	10	22,119	1,072	4.85
1971	36	73,134	1,923	2.63

[a] Calculated from regression equation (Koski 1966), Y = -3,184 + 7.81 X, where X = average length in mm (from unpublished data) and Y = individual fecundity. Total fecundity equals Y times the number of female spawners.

TABLE A-9. ESTIMATED BIOMASS (g/m^2) OF JUVENILE COHO SALMON, DEER CREEK, OREGON, 1959-1968 (FROM CHAPMAN 1965 AND AU 1972). DATA ARE INTERPOLATED FOR THE BEGINNING OF EACH MONTH INDICATED, FROM POPULATION ESTIMATES MADE LESS FREQUENTLY THROUGHOUT THE YEAR.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
June	4.8	2.7	2.1	5.9	4.2	2.1	4.8	5.0	8.7	2.3
July	4.0	2.5	2.5	3.6	3.7	2.1	5.9	4.3	7.2	3.0
Aug	3.1	2.3	3.0	3.0	3.4	2.1	4.3	3.8	6.2	3.7
Sept	2.9	2.3	3.2	4.0	3.1	2.6	3.2	3.6	5.9	4.4
Oct	3.1	2.5	3.4	4.7	2.5	3.1	2.9	3.8	6.1	5.0
Nov	3.6	2.7	3.4	5.1	2.4	3.5	2.8	4.0	6.3	5.3
Dec	3.6	2.0	3.2	4.0	2.4	3.7	2.7	4.1	6.1	5.1
Jan	3.8	2.0	3.8	4.5	2.5	3.6	3.0	4.2	4.4	4.1
Feb	4.0	2.0	1.7	4.5	2.5	2.8	2.9	4.2	3.5	2.9
Mar	4.2	2.0	1.7	3.6	2.4	1.9	2.4	3.7	3.2	2.2
Apr	1.8	1.3	1.3	2.1	1.6	1.5	0.8	1.9	1.9	1.4
May	0.5	0.4	0.6	0.5	-	-	-	-	-	-

TABLE A-10. ESCAPEMENT, POTENTIAL EGG DEPOSITION, AND FRESHWATER SURVIVAL OF COHO SALMON, FLYNN CREEK, OREGON, 1959-1971 (FROM KNIGHT 1980).

Brood Year	Female Escapement	Egg Potential[a]	Smolt Count	Freshwater Survival (%)
1959	8	17,368	875	5.04
1960	26	66,742	776	1.16
1961	51	131,427	1,354	1.03
1962	2	4,644	565	12.17
1963	20	44,220	736	1.66
1964	10	24,020	663	2.76
1965	11	26,565	968	3.64
1966	55	138,050	616	0.45
1967	10	23,130	430	1.86
1968	19	38,931	207	0.53
1969	5	9,625	140	1.45
1970	5	13,745	330	2.40
1971	18	37,404	404	1.08

[a] Calculated from regression equation (Koski 1966), $Y = -3{,}184 + 7.81\,X$, where X = average length in mm (from unpublished data) and Y = average individual fecundity. Total fecundity equals Y times the number of female spawners.

TABLE A-11. ESTIMATED BIOMASS (g/m^2) OF JUVENILE COHO SALMON, FLYNN CREEK, OREGON, 1959-1968 (FROM CHAPMAN 1965 AND AU 1972). DATA ARE INTERPOLATED FOR THE BEGINNING OF EACH MONTH INDICATED, FROM POPULATION ESTIMATES MADE LESS FREQUENTLY THROUGHOUT THE YEAR.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
June	4.1	2.9	2.1	8.3	1.3	2.2	4.1	4.0	6.0	1.1
July	3.3	2.8	2.0	3.0	1.7	1.7	1.7	2.8	3.9	1.3
Aug	3.0	2.7	2.1	2.3	2.0	1.5	1.4	2.6	2.9	1.8
Sept	3.1	2.6	2.3	2.6	2.2	1.7	1.6	2.9	2.1	2.3
Oct	2.9	2.5	2.5	3.4	2.4	1.8	1.7	2.8	1.8	2.5
Nov	2.9	2.5	2.5	3.8	2.2	2.0	1.7	2.6	1.7	2.3
Dec	2.4	2.0	3.5	4.5	2.0	1.9	1.7	2.4	1.7	1.8
Jan	2.2	1.9	2.1	4.1	1.8	1.9	1.7	2.5	1.8	1.1
Feb	2.2	1.7	2.0	4.1	1.6	1.7	1.6	2.5	1.7	0.9
Mar	2.6	1.8	1.8	3.8	1.4	1.7	1.1	2.1	1.6	0.8
Apr	1.5	1.7	1.6	2.6	1.1	1.3	0.4	0.9	1.4	0.5
May	0.5	1.3	0.7	1.4	-	-	-	-	-	-

TABLE A-12. ESCAPEMENT, POTENTIAL EGG DEPOSITION, AND FRESHWATER SURVIVAL OF COHO SALMON, NEEDLE BRANCH, OREGON, 1959-1971 (FROM KNIGHT 1980).

Brood Year	Female Escapement	Egg Potential[a]	Smolt Count	Freshwater Survival (%)
1959	2[b]	4,471[b]	462	10.3
1960	2	4,192	223	5.32
1961	15	33,135	470	1.42
1962	4	9,632	314	3.26
1963	15[c]	33,530[d]	160	0.477
1964	25[c]	55,884[d]	286	0.512
1965	28[c]	62,590[d]	333	0.532
1966	19	46,664	277	0.594
1967	15	40,460	421	1.04
1968	17	35,088	194	0.55
1969	1	2,666	76	2.85
1970	2	5,386	113	2.10
1971	18	35,604	369	1.04

[a] Calculated from regression equation (Koski 1966), Y = -3,184 + 7.81 X, where X = average length in mm (from unpublished data) and Y = average individual fecundity. Total fecundity equals Y times the number of female spawners.

[b] Estimated equivalents from 1,627 planted fry.

[c] Estimated from redd surveys.

[d] Estimated from mean female length (693.9 mm) from the other years of the study.

TABLE A-13. ESTIMATED BIOMASS (g/m^2) OF JUVENILE COHO SALMON, NEEDLE BRANCH, OREGON, 1959-1968 (FROM CHAPMAN 1965 AND AU 1972). DATA ARE INTERPOLATED FOR THE BEGINNING OF EACH MONTH INDICATED, FROM POPULATION ESTIMATES MADE LESS FREQUENTLY THROUGHOUT THE YEAR.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
June	2.3	1.4	2.1	7.2	3.5	4.0	5.0	7.6	6.9	3.1
July	1.6	1.7	1.9	3.9	3.0	2.4	3.9	4.0	9.0	3.4
Aug	1.8	2.0	1.8	3.2	2.9	1.5	3.5	3.1	7.8	3.8
Sept	1.9	2.0	1.8	2.8	2.7	1.3	3.4	3.7	6.5	4.2
Oct	2.2	2.2	1.7	2.8	2.8	1.2	3.3	4.3	6.2	4.6
Nov	2.4	2.4	1.7	2.9	2.7	1.0	2.9	4.1	3.2	4.4
Dec	2.0	2.2	1.8	2.8	2.6	0.7	2.2	4.4	3.1	3.7
Jan	1.9	2.2	1.8	3.3	2.3	0.8	1.9	4.0	3.2	2.4
Feb	1.9	2.4	1.7	3.1	2.3	0.9	1.3	3.1	3.9	1.7
Mar	2.4	1.5	1.4	3.1	1.5	1.0	0.8	1.5	2.6	0.4
Apr	2.4	1.1	1.8	2.1	1.0	0.8	0.4	0.4	0.2	0.1
May	0.9	0.3	0.7	0.9	-	-	-	-	-	-

TABLE A-14. BIOMASS (g/m^2 IN SEPTEMBER) OF CUTTHROAT TROUT, ALSEA WATERSHED STUDY, 1962-1973 (FROM LOWRY 1964 AND UNPUBLISHED DATA)

Year	Deer Cr.	Flynn Cr.	Needle Br.
1962	5.07	5.82	3.89
1963	2.93	3.54	3.41
1964	1.90	4.04	3.16
1965	2.93	2.72	2.97
1966	2.05	2.73	1.09
1967	3.29	4.26	0.68
1968	2.15	2.71	1.65
1969	2.80	3.70	1.46
1970	3.83	4.01	1.14
1971	4.20	4.27	1.32
1972	4.03	4.13	1.39
1973	-	3.79	1.53

TABLE A-15. BIOMASS (g/m^2) OF SALMONID SPECIES IN THREE NORTHERN CALIFORNIA STREAMS, 1967-1969 (FROM BURNS 1971).

	No. Fork, Casper Cr.		S. Fork Yager Cr.	Godwood Cr.	
	Coho	Steelhead	Steelhead	Coho	Trout[a]
June 1967	0.18	1.09	-	-	-
July 1967	-	-	-	1.09	0.57
Aug 1967	-	-	3.22	-	-
Oct 1967	0.15	1.46	-	-	-
June 1968	0.13	1.16	-	-	-
July 1968	-	-	-	0.76	0.49
Aug 1968	-	-	4.21	-	-
Oct 1968	0.19	1.44	-	-	-
June 1969	0.61	0.98	-	-	-
July 1969	-	-	-	0.34	0.51
Aug 1969	-	-	2.94	-	-
Oct 1969	0.81	1.13	-	-	-

[a] Steelhead and cutthroat.

TABLE A-16. BIOMASS OF BROOK TROUT (g/m^2 IN MID-AUGUST) IN 10 SECTIONS OF SAGEHEN CREEK, CALIFORNIA, 1952-1961 (FROM R. GARD PERS. COMM.). SECTION I IS UPSTREAM.

	I	II	III	IV	V	VI	VII	VIII	IX	X
1952	5.15	13.90	3.75	1.48	0.39	0.80	2.01	1.06	0.24	0.01
1953	4.71	14.24	4.74	1.38	0.50	3.25	1.46	0.67	0.07	0
1954	4.85	10.12	2.17	1.28	0	1.29	1.01	1.60	0	0
1955	4.48	6.87	2.45	0.41	0.01	0.74	0.06	1.31	0	0
1956	2.47	6.65	1.80	0.96	0.18	0.55	0.41	0.13	0.01	0
1957	4.56	3.67	1.88	1.49	0.25	0.80	0.18	0.19	0	0
1958	2.24	2.91	1.23	0.25	0.53	1.14	0.96	1.84	0	0
1959	-	7.40	2.31	0.85	0.35	1.78	0.24	0.19	0.01	0
1960	4.63	2.32	1.95	0.19	0.54	1.64	0.86	0.75	0	0
1961	3.36	2.50	0.86	1.12	0.55	2.85	1.56	0.40	0	0

TABLE A-17. BIOMASS OF BROWN TROUT (g/m^2 IN MID-AUGUST) IN 10 SECTIONS OF SAGEHEN CREEK, CALIFORNIA, 1952-1961 (FROM R. GARD PERS. COMM.). SECTION I IS UPSTREAM.

	I	II	III	IV	V	VI	VII	VIII	IX	X
1952	0	0	0	0	0	0	0.63	8.56	1.99	0.40
1953	0	0	0	0	0	0.08	6.34	1.18	1.18	0.78
1954	0	0	0	0	0	0	1.69	1.47	2.03	0.67
1955	0	0	0	0	0	0.01	3.96	1.66	4.18	0.45
1956	0	0	0	0	0	0	1.48	1.06	2.54	0.11
1957	0	0	0	0	0	0.44	0.91	0	2.95	0.01
1958	0	0	0.54	0	0	0.08	0	0.13	4.11	0.16
1959	-	0	0	0	0	0.02	1.30	1.97	2.82	0
1960	0	0	0	0	0.06	0	1.30	0.37	2.93	0
1961	0	0	0	0	0	0.02	1.51	0.16	1.74	0.01

TABLE A-18. BIOMASS OF RAINBOW TROUT (g/m^2 IN MID-AUGUST) IN 10 SECTIONS OF SAGEHEN CREEK, CALIFORNIA, 1952-1961 (FROM R. GARD PERS. COMM.). SECTION I IS UPSTREAM.

	I	II	III	IV	V	VI	VII	VIII	IX	X
1952	0	1.12	1.45	4.69	0.75	1.01	0.99	0.54	0.21	0.07
1953	0	1.27	4.30	4.78	0.77	1.20	1.46	0.99	0.28	0.03
1954	0	1.42	2.31	3.89	0.37	1.73	2.42	0.45	0.01	0
1955	0	1.04	2.82	4.07	0.31	2.26	1.43	0.77	0	0.12
1956	0	0.41	1.30	2.21	0.45	1.75	0.41	0.05	0	0
1957	0	1.09	1.23	3.45	0.44	2.93	1.82	0.64	0.15	0
1958	0	1.12	0.91	2.35	1.43	3.55	1.79	0.75	0.59	0.07
1959	-	1.04	0.54	4.02	0.37	5.30	2.50	0.91	0	0
1960	0	0.37	0.83	4.60	0.83	4.29	1.54	0.11	0.49	0
1961	0	0.41	0.36	5.91	0.89	6.67	1.64	0.96	0	0

TABLE A-19. ESCAPEMENT, POTENTIAL EGG DEPOSITION, AND FRESHWATER SURVIVAL OF COHO SALMON, WADDELL CREEK, CALIFORNIA, 1933-1940 (FROM SHAPOVALOV AND TAFT 1954).

Brood Year	Female Escapement	Egg Potential	Smolt Count	Freshwater Survival (%)
1933	222	560,690	3,573	0.64
1934	309	725,014	4,911	0.68
1935	59	141,233	1,067	0.76
1936	157	377,352	1,926	0.51
1937	37	91,728	852	0.93
1938	56	130,074	1,740	1.34
1939	150	396,321	152	0.038
1940	115	257,886	711	0.28

TABLE A-20. DOWNSTREAM TRAP COUNTS OF STEELHEAD TROUT BY AGE GROUP, WADDELL CREEK, CALIFORNIA, 1933-1942 (FROM SHAPOVALOV AND TAFT 1954).

Year	0		I		II		III	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1933-34	604	19	741	24	1,657	53	112	4
1934-35	699	39	578	32	484	27	28	2
1935-36	1,365	35	1,655	42	830	21	90	2
1936-37	1,875	53	1,191	34	451	13	11	a
1937-38	1,946	57	1,015	30	410	12	19	1
1938-39	691	11	3,699	60	1,720	28	77	1
1939-40	2,239	64	945	27	292	8	7	a
1940-41	3,306	59	2,049	36	251	4	9	a
1941-42	2,009	35	2,834	50	843	15	33	1

a < 1 percent.

TABLE A-21. BIOMASS (g/m^2) OF BROOK, RAINBOW, AND BROWN TROUT, TROUT CREEK, MONTANA, 1950-1951 (FROM HOLTON 1953). SECTION 1 IS UPSTREAM.

Section	1				2					3					4			
Date	Aug. 24 1950	Nov. 18 1950	May 20 1951	Aug. 12 1951	July 25 1950	Sept. 14 1950	Nov. 19 1950	May 30 1951	Aug. 4 1951	Aug. 9 1950	Sept. 14 1950	Nov. 4 1950	June 3 1951	Aug. 11 1951	Aug. 1 1950	Oct. 28 1950	May 17 1951	Aug. 5 1951
Brook	13.0	34.9	12.4	10.8	3.8	8.0	3.7	2.1	5.3	2.2	2.1	3.4	1.3	2.1	2.1	1.4	1.1	0.2
Rainbow	2.0	3.0	0.9	0.9	3.6	6.5	5.0	6.6	8.1	4.9	5.0	5.8	6.9	5.7	3.9	6.4	3.0	6.2
Brown	0	0	0	0	0.4	0.8	4.6	6.7	8.4	0.5	0.5	10.6	0.1	0.3	0.6	9.7	4.1	0.7

TABLE A-22. BIOMASS (g/m^2) OF BROWN, RAINBOW, AND BROOK TROUT IN 11 SECTIONS OF LITTLE PRICKLY PEAR CREEK, MONTANA, SUMMER 1966 (FROM ELSER 1968). SECTION 1 IS UPSTREAM

Section	1A	1	2	3	4[a]	5	6[a]	7	8[a]	9	10[a]
Area (m^2)	2388	1093	1862	2266	2995	2630	3157	2145	1740	1255	3238
Mean width (m)	5.5	2.7	5.5	7.3	7.6	8.2	8.8	7.3	6.4	7.6	13.4
Brown	1.57	3.14	12.9	16.7	3.36	17.6	4.37	17.1	10.4	11.1	1.57
Rainbow	4.70	5.04	5.60	5.72	0.90	6.39	2.02	7.85	1.91	5.94	4.04
Brook	1.01	10.8	3.81	2.02	0.22	0.45	0.11	0.34	0.67	0.22	0.11
Total trout	7.28	19.0	22.3	24.4	4.48	24.4	6.50	25.3	13.0	17.3	5.72

[a] Altered sections.

TABLE A-23. NUMBER OF CUTTHROAT TROUT TRAPPED, AND NUMBER REMAINING IN STREAM AFTER TRAP WAS REMOVED,[a] ARNICA CREEK, YELLOWSTONE PARK, WYOMING, 1950-1958 (FROM BENSON 1960).

Year	Date trap removed	Age-group 0		Age-group I		Age-group II		Total		Grand Total
		Trapped	In Stream	Trapped	In Stream	Trapped	In Stream	Trapped	In Stream	
1950	Sept. 28	9,556	-	300	-	95	-	9,951	-	9,951
1951	Oct. 6	5,240	-	365	-	39	-	5,644	-	5,644
1952	Sept. 21	502	-	792	-	242	-	1,536	-	1,536
1953	Sept. 28	1,332	708	763	407	82	67	2,177	1,182	3,359
1954	Sept. 14	4,151	-	943	-	47	-	5,141	-	5,141
1955	Sept. 24	4,182	244	340	15	7	0	4,529	259	4,788
1956	Sept. 13	4,268	612	386	56	132	5	4,786	673	5,459
1957	Sept. 25	2,850	405	121	270	5	3	2,976	678	3,654
1958	Aug. 31	36	1,950	9	30	1	15	46	1,995	2,041

[a] Data not available on number of fish in stream after dismantling of trap for 1950, 1951, 1952, and 1954.

TABLE A-24. BIOMASS (g/m^2) OF BROOK TROUT, LAWRENCE CREEK, WISCONSIN, 1953-1957 (FROM McFADDEN 1961b). SECTION A IS UPSTREAM.

	Section					
	A	B	C	D	Total	Mean
Sept. 1953	10.30	9.81	8.40	5.52	34.03	8.51
Sept. 1954	14.53	12.36	8.81	6.31	42.01	10.50
April 1955	11.18	9.64	6.82	6.60	34.24	8.56
Sept. 1955	7.11	8.25	6.10	3.02	24.48	6.12
April 1956	4.41	4.27	3.89	2.45	15.02	3.75
Sept. 1956	10.76	6.01	5.50	1.30	23.57	5.89
April 1957	14.48	6.93	5.35	3.37	30.13	7.53
Sept. 1957	26.18	10.74	6.37	4.20	47.49	11.87

TABLE A-25. SEPTEMBER POPULATION ESTIMATES OF AGES 0 AND I BROOK TROUT IN LAWRENCE CREEK AND BIG ROCHE-A-CRI CREEK, WISCONSIN, 1953-1964 (FROM WHITE AND HUNT 1969).

Year	Lawrence Creek		Big Roche-a-Cri Creek	
	0	I	0	I
1953	10,113	2,040	-	-
1954	13,523	2,749	-	-
1955	5,720	2,754	-	-
1956	10,853	816	-	-
1957	13,258	3,370	2,012	1,135
1958	4,166	4,393	6,229	474
1959	22,646	1,044	2,637	1,817
1960	8,507	3,324	9,915	1,257
1961	14,313	2,360	4,361	2,630
1962	7,611	4,523	5,632	1,609
1963	10,367	2,388	4,964	1,623
1964	9,680	4,382	7,420	1,072

TABLE A-26. BIOMASS (g/m^2)[a] OF BROOK TROUT BY AGE GROUP IN APRIL AND SEPTEMBER, LAWRENCE CREEK, WISCONSIN, 1960-1970 (FROM HUNT 1974).

Year	April					September					
	I	II	III	IV+	Total	0	I	II	III	IV+	Total
1960	4.00	0.375	0.542	0.0245	4.94	2.01	4.75	0.105	0.0417	0	6.91
1961	1.97	1.48	0.0245	0.0294	3.50	3.83	4.39	0.922	0.0172	0	9.16
1962	5.48	2.30	0.412	0.0049	8.20	1.70	6.08	0.507	0.0980	0	8.38
1963	2.71	4.62	0.333	0.0858	7.75	2.80	3.39	1.78	0.137	0.0392	8.15
1964	5.20	2.72	1.20	0.108	9.23	2.51	5.56	0.995	0.387	0.0319	9.48
1965	2.48	3.30	0.517	0.174	6.47	2.18	4.30	1.13	0.167	0.0294	7.81
1966	3.96	3.38	0.934	0.130	8.40	2.54	6.19	1.64	0.299	0.0392	10.7
1967	3.15	5.65	1.04	0.427	10.3	2.14	4.03	2.02	0.302	0.0613	8.63
1968	3.35	4.43	1.62	0.287	9.69	2.85	3.40	0.863	0.280	0.0686	7.46
1969	5.25	3.75	0.699	0.194	9.89	3.10	4.51	1.02	0.177	0.0809	8.89
1970	3.88	5.17	0.701	0.142	9.89	3.32	3.78	0.980	0.145	0.0466	8.27
Mean	3.77	3.38	0.729	0.146	8.02	2.63	4.58	1.09	0.194	0.0361	8.53

[a] Biomass from Appendix Table 1 has been divided by stream area of 4.08 ha.

TABLE A-27. ANNUAL PRODUCTION ($g/m^2/yr$) OF BROOK TROUT BY SECTION AND AGE GROUP, LAWRENCE CREEK, WISCONSIN, 1960-1970 (FROM HUNT 1974). SECTION A IS UPSTREAM.

Year	Section				Age Group					Stream Total
	A	B	C	D	0	I	II	III	IV+	
1960	13.0	10.1	13.4	14.0	4.1	7.7	0.3	0.4	<0.1	12.5
1961	17.2	13.5	10.2	8.0	6.8	3.9	1.1	<0.1	0.1	11.9
1962	14.0	10.0	11.1	10.8	3.8	6.2	0.9	0.2	<0.1	11.2
1963	16.5	12.0	12.9	11.5	6.4	4.0	2.2	0.2	<0.1	12.9
1964	19.8	12.8	9.8	8.6	5.2	5.2	1.2	0.5	<0.1	12.2
1965	19.5	9.8	11.0	5.4	4.3	4.2	1.9	0.2	<0.1	10.6
1966	15.2	12.6	9.8	6.3	3.1	5.7	1.4	0.4	<0.1	10.6
1967	21.7	9.4	10.9	6.7	3.8	4.5	2.4	0.5	<0.1	11.2
1968	21.3	12.0	8.9	5.1	4.5	4.0	1.9	0.6	0.1	11.1
1969	25.8	12.0	7.9	6.6	4.7	5.3	1.6	0.3	0.1	12.0
1970	20.5	13.2	10.1	7.8	5.3	4.6	2.2	0.2	<0.1	12.3
Mean	18.8	11.6	10.6	8.2	4.8	5.0	1.6	0.3	<0.1	11.7

TABLE A-28. PHYSICAL CHARACTERISTICS AND BIOMASS (g/m^2) OF BROOK, BROWN, AND RAINBOW TROUT IN SECTIONS OF THREE MICHIGAN STREAMS, 1937 (FROM SHETTER AND HAZZARD 1938).

Stream	Section	Length (m)	Mean Width (m)	Mean Depth (cm)	Velocity (cm/sec)	Relative Shade	Biomass Brook	Biomass Brown	Biomass Rainbow	Biomass Total
South Branch, Pine River	Upper	29.5	7.6	24.9	22.9	Partly	0.95	0	0.35	1.30
	Middle	29.0	5.4	27.7	26.2	Densely	0.87	0	0.53	1.40
	Lower	31.5	6.7	34.8	20.7	Partly	2.40	0.27	1.82	4.49
Little Manistee River	Upper	32.5	8.5	43.7	41.8	Partly	0.21	1.92	1.75	3.88
	Middle	46.9	11.2	44.2	-	Exposed	0.12	0.73	2.54	3.39
North Branch, Boardman River	Upper	42.6	7.5	25.7	94.5	Partly	0.028	0.84	0	0.87
	Middle	29.0	8.5	29.0	46.3	Exposed	0.041	0.13	0	0.17
	Lower	37.0	9.1	23.1	51.5	Partly	0.048	0.10	0	0.15

TABLE A-29. NUMBER OF BROOK TROUT PRESENT IN SEPTEMBER IN HUNT CREEK, MICHIGAN BY AGE-GROUP (FROM MCFADDEN ET AL. 1967).

Year	0	I	II	III	IV	Total
1949	4,471	2,036	287	14	0	6,808
1950	3,941	2,013	304	13	0	6,271
1951	4,287	1,851	265	16	1	6,820
1952	5,033	1,763	261	16	0	7,073
1953	5,387	1,637	175	13	0	7,212
1954	6,325	2,035	234	13	0	8,607
1955	4,235	2,325	383	24	0	6,947
1956	4,949	1,612	392	51	1	7,005
1957	6,703	1,796	309	33	1	8,842
1958	5,097	2,653	355	26	2	8,133
1959	4,038	2,395	685	68	0	7,186
1960	5,057	2,217	473	47	1	7,795
1961	2,809	2,017	409	23	0	5,258
1962	5,052	1,589	448	52	2	7,143

TABLE A-30. MEAN ANNUAL BIOMASS (g/m^2) OF BROOK TROUT IN STREAMS IN MATAMEK WATERSHED, QUEBEC, 1971-1973 (FROM O'CONNOR AND POWER 1976).

Stream	Section Length (m)	Average Width (m)	Year	Biomass							
				0+	1+	2+	3+	4+	5+	6+	Total
Kaikhosru	355	6.1	1971	0.35	1.93	0.33	0.54	0.85	0.17	0	4.17
			1972	0.35	2.23	0.66	0.44	0.22	0.06	0	3.96
Gallienne	330	6.6	1971	-	2.40	2.12	0.57	0.14	0.10	0	5.33
			1972	-	2.83	1.74	0.49	0.08	0.14	0	5.28
Tchinicaman	620	15.1	1971	0.08	0.51	0.26	0.25	0.05	0.01	0.06	1.21
			1972	0.08	0.42	0.48	0.32	0.07	0.01	0.03	1.42
Sherry	215	4.2	1971	0.28	1.25	0.87	1.13	0.25	0	0	3.78
			1972	0.28	0.79	0.51	0.30	0.15	0	0	2.03
			1973	0.28	0.57	0.28	0.16	0.17	0	0	1.47

TABLE A-31. NUMBERS OF BROOK TROUT IN A 411-m SECTION OF HAYES BROOK, PRINCE EDWARD ISLAND, 1947-1960 (FROM SAUNDERS AND SMITH 1962).

Year	Age 0	Age I+	Total
1947	588	351	939
1948	729	342	1,071
1949	539	279	818
1950	321	223	544
1951	166	418	584
1952	611	372	983
1953	308	362	670
1954	468	294	762
1955	758	383	1,141
1956	580	467	1,047
1957	350	363	713
1958	481	314	795
1959	371	352	723
1960[a]	526	611	1,137

[a] After habitat development.

TABLE A-32. COUNTS OF ATLANTIC SALMON SMOLTS AND SEAWARD MIGRATING BROOK TROUT, LITTLE CODROY RIVER, NEWFOUNDLAND, 1954-1963 (FROM MURRAY 1968).

Year	Salmon	Trout
1954	12,210	-
1955	11,248	-
1956	14,772	706
1957	8,900	1,067
1958	9,341	889
1959	12,099	1,074
1960	7,829	457
1961	8,058	312
1962	8,193	698
1963	7,326	485

TABLE A-33. BIOMASS (g/m^2) OF BROWN TROUT IN TRIBUTARIES AND THE MAIN STEM OF THE UPPER RIVER TEES SYSTEM, ENGLAND, 1967-1970 (FROM CRISP ET AL. 1974).

	Maize Beck	River Tees below Cauldron Snout	River Tees above the Weel	Weelhead Sike	Dubby Sike	Mattergill Sike	Lodgegill Sike
Section Length (m)	70.9	30.5	23.4	97.5	40.8	47.2	45.7
Mean Width (m)	9.94	6.91	11.20	1.16	1.54	3.26	3.05
Section Area (m^2)	705	211	262	113	63	154	139
August 1967	3.68	3.65	-	3.21	-	5.14	-
October 1967	1.43	2.16	0.08	16.63	6.85	5.84	3.34
May 1968	0.81	1.28	-	2.81	2.55	1.03	0.32
July 1968	0.30	1.28	0.37	3.43	4.69	1.72	0.60
October 1968	0.92	2.24	0.01	4.73	3.20	11.76	5.25
May 1969	0.48	1.11	-	1.96	2.45	1.18	1.87
August 1969	0.42	1.21	-	4.44	4.09	2.68	1.21
October 1969	1.18	0.96	-	5.45	3.14	4.87	1.26
May 1970	1.05	2.05	-	1.56	1.66	1.63	0.57

TABLE A-34. MEAN (1968-1972) BIOMASS (g/m^2) OF BROWN TROUT IN FIVE TRIBUTARIES OF THE RIVER TEES SYSTEM, ENGLAND, IN MAY, AUGUST, AND OCTOBER (FROM CRISP ET AL. 1975).

		Moss Burn	Nether Hearth Sike	Trout Beck	Great Dodgen Pot Sike 'A'	Great Dodgen Pot Sike 'B'
Mean Width (m)[a]		1.9	4.1	5.6	0.9	1.6
Surface Area (m^2)[a]		254	209	205	84	115
May	Minimum	0.8	0.7	1.0	3.0	1.1
	Mean	1.19	1.14	1.45	4.55	1.85
	Maximum	1.6	1.5	1.8	6.8	2.7
August	Minimum	1.4	1.8	2.4	>3.5	1.6
	Mean	2.00	2.62	3.97	5.54	3.77
	Maximum	2.9	3.8	6.2	10.1	7.1
October	Minimum	1.0	1.2	1.0	5.3	2.9
	Mean	1.87	2.02	1.47	5.41	3.88
	Maximum	2.2	2.8	1.9	8.1	5.1

[a] Based on measurements made in May 1968.

TABLE A-35. PRODUCTION (g/m^2) OF ATLANTIC SALMON AND BROWN TROUT IN THREE SECTIONS OF SHELLIGAN BURN, SCOTLAND, 1966-1968 (FROM EGGLISHAW 1970).

	Year Class						Annual Totals	Section Length (m)	Mean Width (m)	Section Area (m^2)
	1963	1964	1965	1966	1967	1968				
Section 1-Upstream								30.8	4.10	126.0
1966 Salmon	0.23	1.57	1.25	4.47	-	-	7.52			
Trout	0.65	1.47	3.42	4.10	-	-	9.64			
1967 Salmon	0	0.11	0.63	2.22	7.88	-	10.84			
Trout	0	0.52	0.77	5.05	5.82	-	12.16			
1968 Salmon	0	0	0.16	0.64	2.53	8.54	11.87			
Trout	0	0	0	0.94	3.10	2.67	6.71			
Section 2								27.9	3.07	86.0
1966 Salmon	0	1.12	1.07	3.52	-	-	5.71			
Trout	0.51	2.49	4.69	2.80	-	-	10.62[a]			
1967 Salmon	0	0.03	0.18	1.92	6.59	-	87.2			
Trout	0	0	2.07	5.95	3.98	-	12.00			
1968 Salmon	0	0	0	0.43	2.51	7.28	10.22			
Trout	0	0	0	1.91	4.40	2.39	8.70			
Section 3-Downstream								27.5	3.43	94.0
1966 Salmon	0	0.51	1.03	4.69	-	-	6.23			
Trout	0.41	1.96	4.44	3.95	-	-	10.76			
1967 Salmon	0	0.30	0.52	2.87	8.59	-	12.28			
Trout	0	0.46	2.02	5.68	4.54	-	12.70			
1968 Salmon	0	0	0	0.72	2.56	7.89	11.17			
Trout	0	0	0	1.45	3.92	2.44	7.81			

[a] Includes 0.13 g/m^2 production of the 1962 year class.

TABLE A-36. BIOMASS (g/m^2) OF ATLANTIC SALMON AND BROWN TROUT AT THE END OF THE GROWING SEASON, SHELLIGAN BURN, SCOTLAND, 1966-1975 (FROM EGGLISHAW AND SHACKLEY 1977). TOTAL BIOMASS INCLUDES ± STANDARD ERROR.

	Salmon				Trout				Total
Year	0+	1+	2+	All	0+	1+	2+	All	Biomass
1966	3.5	1.0	1.5	6.0±1.9	2.5	4.0	3.2	9.8±1.1	15.8±0.9
1967	2.7	1.7	0.2	4.6±1.2	3.6	6.1	1.8	11.4±1.5	16.1±2.6
1968	2.5	1.7	0.7	4.9±0.9	1.9	3.2	0.9	6.0±1.1	10.9±2.1
1969	4.4	2.2	0.7	7.3±1.9	5.0	3.8	2.9	11.6±2.1	18.9±2.8
1970	1.9	2.5	0.3	4.7±2.3	1.9	6.0	2.1	10.1±2.5	14.8±3.9
1971	4.7	2.4	0.5	7.6±1.9	3.8	4.9	1.4	10.1±2.9	17.7±4.2
1972	2.6	4.6	0.3	7.5±2.8	3.2	6.9	0.8	10.9±2.0	18.4±4.2
1973	3.7	3.8	0.2	7.6±1.4	4.0	5.4	1.2	10.7±2.5	18.3±3.2
1974	3.2	3.4	0.0	6.6±1.2	2.5	4.5	0.4	7.4±2.2	14.0±3.2
1975	6.1	2.9	0.2	9.2±2.6	1.9	4.3	0.8	7.1±2.1	16.3±4.0
Mean	3.5	2.6	0.5	6.6±1.5	3.0	4.9	1.6	9.5±2.0	16.1±2.4

TABLE A-37. BIOMASS (g/m^2) OF BROWN TROUT IN SIX SECTIONS OF HOROKIWI STREAM, NEW ZEALAND, 1940-1941 (FROM ALLEN 1951). SECTION I IS DOWNSTREAM.

Zone Length (m)	I 3,167	IIM 2,035	IIR 1,918	III 2,719	IV 1,602	V 527	Total
July 1940	24.1	31.5	11.7	24.9	41.0	18.8	25.6
Oct. 1940	28.0	36.1	11.7	25.7	46.4	24.7	28.6
Jan. 1941	34.1	32.7	11.0	16.4	29.8	21.9	26.5
May 1941	22.8	42.8	14.9	21.3	26.0	24.4	25.8
Oct. 1941	1.8	13.7	2.5	2.7	18.7	18.5	6.5